Effects of landscape fragmentation on bird communities in a tropical hotspot

Dissertation

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1 General Introduction

Fragmentation influences biodiversity

There is large evidence that habitat loss and landscape fragmentation is one of the main drivers of biodiversity loss (e.g. Debinski and Holt 2000; Koh and Ghazoul 2010; Sodhi et al. 2004: Pardini et al. 2010), influencing the functionality of the habitats in a given landscape (Fahrig 2013) and leading to changes in ecosystems (Hooper et al. 2012). Besides, changes in land use are no longer considered a local environmental phenomenon, but are becoming globally important (Foley et al. 2005) and are seen as a major impact on biodiversity and ecosystem processes around the world (Sala et al. 2000). Newer techniques, such as remote sensing, are revealing that land-use change strongly influences fragmentation patterns (Nagendra et al. 2004). Consequently, the managers of natural areas and conservationists are facing high rates of biodiversity loss and landscape modification with negative consequences for ecosystem services. Thus, it is imperative to begin to understand the effects of these global changes on biodiversity patterns.

Landscape fragmentation in a hotspot

There are 25 world "hotspots"; a hotspot is determined as a region with an exceptional level of biodiversity, particularly endemism, but that at the same time suffers from high levels of habitat loss (Myers et al. 2000). The Tropical Andes rank first among all hotspots. It is the richest and most diverse region, with greatest concentration of restricted-range bird species, and unfortunately, it is also the place with the highest concentration of the world's threatened bird species (Stotz et al. 1996; Stattersfield et al. 1998; Myers et al. 2000). The latter is mostly due to the high levels of deforestation, agricultural expansion, and urbanization in the region (Wege and Long 1995; Etter and van Wygaarden 2000; Sarmiento 2000; Sarmiento and Frolich 2002). More recently, also global climatic change is promoting habitat changes in the Tropical Andes, as the region

is predicted to become more seasonal with considerable effects on habitat configuration (Foster 2001; Barnett et al. 2005; Sekercioglu 2006).

The Tropical Andes have thus become a priority region for conservation efforts (Wege and Long 1995; Myers et al. 2000). So far, the high-altitude Andes are predicted to suffer dramatic changes from both land use and climate change (Herzog et al. 2012). Here, habitat loss is already widespread and persistent (Hofstede et al. 2002). Further habitat loss is predicted through altitudinal range shifts due to climatic changes, as organisms from lower ranges expand at the expense of higher habitats, which will contract (i.e. montane cloud forest, páramo, cushion páramo, *Polylepis* forest; Herzog et al. 2012). Moreover, habitat loss results from changes in land-use (i.e. burning to promote grazing, introduction of exotic plants, road construction; Sarmiento 2000; Hofstede et al. 2002; Herzog et al. 2012). These changes may result in a loss of biodiversity, homogenization of vegetation types, a further increase in the degree of human intervention and landscape fragmentation (Herzog et al. 2012). Protected areas therefore become important tools for the conservation of natural habitats, both in terms of the biological diversity they contain, and the ecosystem services they provide (Armenteras et al. 2003; Hannah et al. 2007).

Ecuador is part of the Tropical Andes region and is one of the most biologically diverse countries in the world (Jørgensen and León-Yánez 1999). Within Ecuador, the Ecuadorian National System of Protected Areas retains areas of intact vegetation patches, albeit surrounded by matrices of modified landscapes (Mateo et al. 2013). These modified landscapes have long been altered by traditional agricultural and pastoral practices and have been intensified by recent modernization and increased population pressure (Hofstede et al. 2002; Mateo et al. 2013). However, these altered matrices still have a

high potential value in order to connect habitats in fragmented landscapes (Mateo et al. 2013).

Birds and their habitat specialization as responses in a fragmented landscape

Responses of important animal groups, such as birds, towards landscape modification and fragmentation are a good tool for developing and evaluating conservation plans. In fact, the avifauna is often well-studied in fragmented landscapes (Tews et al. 2004). For instance, McKinney and Lockwood (1999) suggest that bird habitat guilds, such as grassland generalists and open-habitat generalists, are well adapted to agroforestry practices and have benefited from global habitat modification and environmental disturbances. This same process, however, promotes the loss of endemic species and habitat-specialist birds such as forest frugivores, migratory insectivores, some grassland specialists and low-mobility inner forest species. Hence, birds grouped into ecologically similar species, such as habitat guilds, could be good for evaluating responses of communities in altered landscapes (Tews et al. 2004; Lloyd and Marsden 2011; Neuschulz et al. 2013).

Birds in the Andean region show very specific adaptations over altitudinal gradients and also to specific local areas (Poulsen and Krabbe 1998; Cahill and Matthysen 2007). Furthermore, across the Ecuadorian Andes, studies carried out in same range altitude of local forests showed that species richness within forests varies little with latitude, although species composition between these localities shows low similarity (Poulsen and Krabbe 1998). Hence, the use of guilds, e.g. related to habitat specialization, could be a good alternative for exploring diversity patterns in the region in addition to taxonomic diversity (i.e. species richness, abundance per species). Furthermore, the high-altitude

Andes of Ecuador, especially the páramo grassland ecosystem show relative low species richness, in comparison with lower habitats (Chapman 1926; Carrión 2000). In this case, the interpretation of taxonomic diversity could lead to a significant underestimation of the effect of landscape fragmentation, habitat loss and environmental disturbance. Consequently, given the narrow habitat adaption of Andean birds, the affinity towards a habitat should be considered as an indicator for research and conservation programs as well. The use of these habitat guilds may improve our understanding of the effects of habitat modification at the community level.

Aim of the thesis

This study is oriented towards understanding the effects of changes in land-use (i.e. road infrastructure) and habitat configuration (i.e. landscape heterogeneity) in a fragmented landscape on high-altitude bird communities of the southern Andes in Ecuador. More specifically, I used structural characteristics of fragmented *Polylepis* woodland, the habitat heterogeneity of the páramo matrix and the proximity of a road through the páramo grassland to explore effects on a bird community and on four different habitat-specialized guilds (i.e. páramo specialists, shrubby páramo specialists, *Polylepis* forest specialists and generalists). I hypothesized a loss in species richness in highly disturbed areas (i.e. roadsides) due to habitat modification and introduction of non-native plants as well as an increase in the abundance of generalists with changes in the bird community composition. Furthermore, well developed *Polylepis* patches (i.e. bigger areas, non-irregular shapes, heterogeneous vegetation composition) and more habitat-complexity of the surrounding páramo grassland (i.e. increasing proportion of native woody plants, well-developed vegetation profile) should increase the connectivity through encouraging movement of the bird community between *Polylepis* patches and the patch-páramo matrix. In particular, the *Polylepis* forest specialists will be more abundant in bigger,

closer patches as well as in areas with more heterogeneous surrounding páramo grassland and more heterogeneous *Polylepis* patches.

Study area

The study area is located in Cajas National Park (CNP) 35 km west of Cuenca, Azuay province at 2°50'S, 79°13'W. It covers an area of 28,544 ha and an elevation range from 3,160 m to 4,445 m (Delgado et al. 2006). Topography of the region is irregular with evidence of past glaciations, where U-shaped valleys and steep slopes are common (>35 degrees, Harden and Borrero 2005; Delgado et al. 2006). I chose CNP as the study area for three main reasons: 1) its important value for bird conservation; the CNP is the only protected area located in the west of the Southern Andes of Ecuador (MAE 2011) and supports a representative avifauna of the high-altitude Andes (Ridgely and Greenfield 2001; Tinoco and Astudillo 2007). The park forms part of two endemic bird centers (Central Andean Páramo and Southern Central Andes, Stattersfield et al. 1998), and is recognized as a key area for bird conservation in Ecuador (Wege and Long 1995; Krabbe et al. 1998), as well as a priority conservation area of *Polylepi*s forest bird species (Fjeldså 2002). Furthermore, the CNP has been declared as a Ramsar site (Ramsar Convention 2013) and is included on the Important Bird Areas list (Devenish et al. 2009); 2) the park contains the highest cover of *Polylepis* woodland in central-southern Ecuador (DIFORPA 2001; Baquero et al. 2004; Minga and Verdugo 2007), with >1000 patches of varying sizes (< 1 ha-44 ha) throughout the páramo grassland. Another consideration was that the páramo grassland, at a finer scale, shows high heterogeneity, with different habitat types occurring (i.e. páramo grassland dominated by *Chalamagrostis bunches*, cushion páramo dominated by *Plantago* and *Oreobolus*, and semi-open shrubby páramo characterized by native woody plants such as *Gynoxis*, *Bracyotum*, *Miconia*, *Chuquiraga*, *Dilostephium* and *Hesperomeles*); 3) despite its importance for bird conservation and its

protection status, the CNP suffers from several stressors related to traditional agricultural practices such as fires to promote grazing (Samaniego et al. 2013), modern anthropogenic pressures such as increasing touristic activities (Rodríguez 2008) as well as the introduction of non-native plants; however, perhaps the most important stressor in the CNP is the highly transited road which passes through 15 km of the páramo ecosystem.

Objectives

The general objective of this study was to explore the responses, at a community level, of high-altitude Andean birds facing the spatial heterogeneity of the fragmented páramo landscape as well as the proximity of the road as a major stressor.

In the second chapter, I investigated the effects of the road infrastructure that passes through 15 km of the páramo ecosystem in CNP. I used two regular distances from the road to explore changes in community composition and also in abundance of habitat-specialist guilds. Specifically, I examined whether the abundance of generalist birds (which use several habitat types) increased with proximity to the road and how this is related to habitat modification at the roadsides. This pattern may lead to changes in community composition which is influenced by the road due to habitat modification.

In the following sections I focused on *Polylepis* patches and also the surrounding páramo. In the third chapter, I used a novel network approach to investigate the connectivity of 15 *Polylepis* patches. I hypothesized that patches can be directly connected via species which occurred in a given patch, and indirectly by species which shared patches in a given landscape. More specifically, I used centrality measures to identify nodes (*Polylepis* patches) which are important connectors of network structure for habitat-specialized guilds. Furthermore, the centrality measure for each habitat-

specialist guild depends on specific likings related to altitudinal distribution of patches, their habitat structure as well as their vegetation composition.

Within this context, in the fourth chapter, I used bird movements and shared species between patch and matrix among the same 15 *Polylepis* patches to further explore connectivity in this fragmented landscape. I hypothesized that bigger patch area, lower patch isolation and more heterogeneous páramo matrix should promote the connectivity of the landscape. More specifically, I suggested that the *Poylepis* forest specialists increase the number of movements when the páramo surrounding the patches are structurally complex, which in turn promotes community similarity between the *Polylepis* patches and their páramo matrix.

The three chapters in the present study haven either been published or preparing to submit in scientific journals. Chapters 2, 3 and 4 can be read independently.

2 The impact of roads on the avifauna of páramo grassland in Cajas National Park, Ecuador

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Abstract

National parks are an important tool for conserving biodiversity, particularly in areas of high biodiversity and endemism such as the tropical Andes. However, national parks often face a variety of stressors related to recreation, road construction and illegal extraction of natural resources. Unfortunately, the influence of these stressors for biodiversity is rarely well documented. Cajas National Park in Ecuador is no exception: Despite being traversed by the Cuenca-Molleturo-Naranjal road, effects of the road construction on biodiversity have not been determined. We therefore assessed the influence of road proximity on bird species richness and abundance as well as composition of bird habitat groups in Cajas National Park using transect walks at 25 m and 250 m distance to the road (overall 18 transects, each 1 km length). In total, we recorded 1110 individuals of 28 páramo bird species. Overall species richness did not differ between transects near and far from the road. Nevertheless, the average abundance of shrubby páramo species was significantly higher far from the road than near the road (Far= 36, Near= 25). Moreover, we found a tendency towards differences in the composition of bird habitat groups between transects near and far from the road. One aspect potentially driving the observed patterns was the increasing proportion of planted non-native woody tree species within páramo grassland near the road, which may have caused reduced abundances of shrubby páramo bird species there. While roads showed a clear impact on the composition of bird species in the páramo, the major effect seems to be driven by the introduction of non-native plant species along the roadside. In order to reduce the impact of roads to a minimum, we suggest that park managers should control the introduction of such plant species.

2 – Impacts of Roads

Introduction

The Tropical Andes bioregion is known for its high concentration of restricted-range bird species and threatened bird species, and ranks first among the world's 25 hotspots of biodiversity (Stotz et al. 1996; Stattersfield et al. 1998; Myers et al. 2000). Ecuador is part of this diverse bioregion, which has been strongly altered by anthropogenic activities such as burning to promote livestock forage, cultivation, introduction of exotic trees, urbanization and road building (Hofstede et al. 2002) with negative effects on biodiversity (Sierra et al. 1999). Protected areas, such as national parks, within this bioregion are consequently vital for the conservation of species and ecosystems. However, even national parks suffer from various stressors linked to recreation, road construction and illegal extraction of natural resources.

In particular, road infrastructure and vehicular traffic have been shown to negatively affect various groups of organisms (e.g., Forman et al. 2002; Fahrig and Rytwinski 2009). Several studies have reported reduced abundance and species richness of birds near roads (Forman and Alexander 1998; Ortega and Capen 1999; Fahrig and Rytwinski 2009; Kociolek and Clevenger 2011). However, other studies have revealed an increase in bird abundance and richness near roads (Cursach and Rau 2008; Fahrig and Rytwinski 2009). Divergent patterns in the effects of roads on abundance and richness of birds may be explained by diverging responses of specific habitat group (Fraterrigo and Wiens 2005). For example, habitat generalist birds have been shown to persist at roadsides (Camp and Best 1993; Fraterrigo and Wiens 2005; Cursach and Rau 2008) whereas understory insectivorous birds may decrease in abundance and richness with increasing proximity to roads (Laurance 2004). Additionally, a number of studies showed that both forest and grassland specialist species decrease in abundance along roads (Forman and Deblinger 2000; Forman et al. 2002; Palomino and Carrascal 2007). More broadly, native bird

species are common in areas with natural vegetation cover whereas introduced species often benefit from roadsides (Clergeau et al. 1998). These patterns suggest that it is important to understand how changes in habitat at the roadsides influence bird communities.

So far, effects of roads on bird communities have not been well documented in the Andean region of Ecuador. Available data from environmental assessments tend to focus on road constructions and maintenance with very limited information on consequences for biodiversity (Mena-Vásconez and Ortiz 2004; Bucheli 2007). Here, páramo grasslands, a particularly distinctive grassland of the tropical Andes region, are the dominant vegetation type in the high Andes (Neill 1999) and harbor approximately 45 restricted-range bird species (Stattersfield et al. 1998; Ridgely and Greenfield 2001) and around 30 globally threatened avian species (BirdLife International 2004). The primary reason for the designation of threatened status of avian páramo species is human degradation of their natural habitats, which includes the construction of roads (Wege and Long 1995; Granizo et al. 2002). Given that degradation of páramo grasslands is an ongoing and unrestricted process (Hofstede et al. 2002), it is imperative to understand how roads impact bird communities. This is particularly important in protected areas so that suitable management strategies can be developed to mitigate these impacts (Reijnen et al. 1997; Forman 2000; Kociolek and Clevenger 2011).

Cajas National Park (CNP) is a protected area located in the southern Andes of Ecuador where the dominant vegetation type is páramo grassland (Minga and Verdugo 2007). A first-order road crosses a northern portion of this ecosystem. This road is heavily transited (P. X. Astudillo, pers. obs.) and was resurfaced in 2009 (Encalada 2009). Our objective was to determine in which way this road influences species richness, abundance, and composition of páramo bird species. We expected a decrease in species

richness and abundance of páramo birds closer to the road due to the introduction of non-native plant species. Moreover, we expected changes in community composition, with habitat generalists (birds which are using several types of habitat) being more common near the road and explore the changes in the community in accordance with the habitat modification at the roadsides.

Materials and methods

Study area

Our study was conducted in Cajas National Park from October 2011 to February 2012. The park is located in the southwestern Andes of Ecuador covering an area of 28 544 ha, with an elevation range of 3,160 to 4,445 m (Delgado et al. 2006). Mean annual precipitation is 1200 mm and monthly temperatures range from 0-20°C (IERSE 2004). The park consists of 90% páramo grassland (Minga and Verdugo 2007). However, the páramo landscape, in the study area, can be classified into four vegetation sub-units (Baquero et al. 2004; Minga and Verdugo 2007): páramo grassland, the most extensive sub-unit, is an open habitat dominated by perennial bunch-grasses (*Calamagrostis*); cushion páramo, an open habitat as well which is dominated by cushion bogs (*Plantago*, *Oreobolus*), this sub-unit covers smaller humid areas; shrubby páramo, a semi-open habitat with a higher vegetation profile with increasing proportion of native woody bushes and shrubs; finally, *Polylepis* woodland, a fragmented woodland with patches of varying sizes (< 1 ha-44 ha) which is dominated by two native *Poylepis* species (*P. incana* and *P. reticulata*).

The Cuenca-Molleturo-Naranjal road passes through 15 km of the páramo ecosystem in the northern section of Cajas National Park at an elevational range of 3,600 to 4,100 m (Supplementary Figure 2.1. see in Appendix). The road is over 40 years old, and has been

reconstructed several times. Infrastructural improvements over the past 10 years have led to an increase in vehicular traffic. There is no formal monitoring of vehicular traffic flow, although between 2005 and 2009 there was an increase in visitors to the park, from 18,000 to 38,000 visitors (Rodríguez 2008; Encalada 2009). Furthermore, the Cuenca-Molleturo-Naranjal road is designed for 700 to 1,500 cars per day (Flores 2013). More importantly, at the roadsides there are several planted groves of non-native *Polylepis* which are located along both sides of the road. The main introduced plant is a species native to Peru, *Polylepis racemosa*, used in Ecuador for reforestation and restoration programs because it shows higher growth rates and greater environmental tolerance than the native *Polylepis* species (CODESAN 2011).

Bird surveys

We established nine strip transects near (~ 25 m) and nine strip transects far (~ 250 m) from the Cuenca-Molleturo-Naranjal road (Supplementary Figure 2.1. see in Appendix). We selected 25 m distance from the road for the near category as transect walks considered birds within 25 m of both sides of each transect (see below) and thus effects of the road up to 50 m from the road could be measured. We selected 250 m from the road for the far category as it is the maximum distance from the road with habitat similar to near the road. Beyond this distance there are many large patches of native *Polylepis* woodland and wetlands (Supplementary Figure 2.1. see in Appendix) that might additionally affect the bird communities. Each transect was 1 km long. We avoided installing transects where the terrain was too irregular to safely count birds (extreme slopes). Each transect was walked three times between October 2011 and February 2012, with at least three weeks between repetitions. We chose transects as they are the best method to quantify birds in open habitats because while the observer walks full attention can be devoted to detecting birds (Ralph et al. 1993). All transects began 15 min after

sunrise and walked at a constant speed for one hour (1km h^{-1}). All birds heard or seen within 25 m of either side of each transect were recorded. Flyovers were excluded. For all bird censuses, two observers worked together with always the same observer conducting the bird censuses, while the second walked zigzags to the 25 m on each side of the transect to flush birds from the grass and shrubs. This technique has been evaluated in previous field expeditions throughout the Andean region and has been found to obtain higher rates of detection than those obtained by one observer (P. X. Astudillo, unpubl. data).

Species were identified using the field guides of Ridgely and Greenfield (2001) and Tinoco and Astudillo (2007). However we followed the October 2013 taxonomic revisions of South American Classification Committee (Remsen et al. 2013). Species were grouped into four habitat preference groups: 1) páramo specialists, which occur in páramo grassland and cushion páramo and prefer more open areas; 2) shrubby páramo specialists which occur in páramo grassland combined with native woody shrubs and prefer areas with taller vegetation profile; 3) *Polylepis* forest specialists; and 4) generalists that use at least two of the aforementioned habitat categories (Table 3.1. see in Appendix).

Vegetation sampling

Along each transect, we classified the vegetation in 20 circular plots. Each plot had a radius of 25 m and the distance between the centers plots was ~50 m. Within each plot, we estimated the percent cover of six vegetation types (Supplementary Table 2.1. see in Appendix): native woody shrubs *Gynoxys* (Asteraceae), *Chuquiraga* (Asteraceae), and *Brachyotum* (Melastomataceae) that are common in the páramo (Minga and Verdugo 2007), non-native plants (mainly *Polylepis racemosa* - Rosaceae) that had been planted along the road when the road was under construction, páramo grassland, cushion páramo

an open habitat dominated by species of cushion bogs such as *Plantago rigida* and *Oreobolus ecuadorensis* and other mosses (Minga and Verdugo 2007), water bodies such as ponds and streams, finally rocky substrates which are naturally present within the study area.

Data analyses

To reduce the number of vegetation variables and thus to condense the description of habitat along the transects (Supplementary Table 2.1. see in Appendix), we did a principal component analysis (PCA). This PCA was based on the on the averaged percentage of vegetation-type cover of the twenty circular plots per transect.

As the bird census had many species with relatively low abundances, we used the Chao1 estimator to obtain a complete richness estimate (Chao 1984) calculated in EstimateS 8.2 (Colwell 2006). We used the mean number of detections of the three surveys per transect as an abundance value (Nur et al. 1999). We tested for an effect of road proximity on estimated species richness using ANOVA. Note that due to the reduced number of species per habitat group we did not analyze them separately (Supplementary Table 3.1. see in Appendix). However, we used MANOVA to test for an effect of road proximity on the abundance of habitat preference groups and the three most abundant species (Zar 1984). All response variables were square root transformed to achieve homogeneity of variances and normality of residuals (Shapiro test: all P values > 0.21).

We applied non-metric multidimensional scaling (NMDS with Bray-Curtis dissimilarity based on abundance data) to explore differences in habitat groups. Furthermore, road proximity and vegetation components (derived from the principal component analysis [PCA]) were post-hoc fitted to each of the two ordination plots and their significance was tested via random permutations (1000 iterations). All statistical

analyses were conducted in R 2.15.2 (R Development Core Team 2011) with alpha= 0.05. We used the 'vegan' package (Oksanen 2011; Oksanen et al. 2011) for the PCA and NMDS.

Results

Vegetation components

We extracted the first two components of the PCA (59.84% of the variance) to characterize the habitat along transects. The first component (PCI) explained 34.83% of the variance and reflected a change from low páramo grassland cover to increasing proportion of non-native plants. The second component (PCII) accounted for 25.01% of the variance and reflected a change from páramo grassland with a higher proportion of native woody shrubs to rocky soils or water bodies (no vegetation, Table 1).

Table 1. Eigenvectors of the principal components analysis of the habitat characteristic of 18 strip transects in Cajas National Park, Ecuador. PCI accounted for 34.83 % of variance and PCII explained 25.01 % of variance.

Habitat variable (%)	PCI	PCII
Woody native shrubs	-0.155	-0.544
Non-native plants	0.842	-0.119
Páramo grassland	-0.836	-0.225
Cushion páramo	0.520	-0.376
Water bodies	-0.480	0.607
Rocky substrates	0.397	0.793

Richness and abundance of birds

In total, we detected 1110 birds of 28 species. The most abundant group of birds classified by habitat preferences was páramo specialists with 47.8% of records (mean = 177 ± 24.3) followed by generalists with 24.6% of detections (mean = 91 ± 5.0), shrubby páramo specialists with 20.8% of counts (mean = 77 ± 11.5), and *Polylepis* forest

specialists with 6.8% of records (mean = 26 ± 3.6). The five most abundant species were *Cinclodes fuscus* with 20.5% of detections (mean = 76 ± 16.0), *Phrygilus unicolor* with 17.1% of counts (mean = 63 ± 17.3), *Asthenes flammulata* with 10.7% of records (mean = 40 ± 8.5), *Grallaria quitensis* with 7.2% of detections (mean = 27 ± 3.2), and *Chalcostigma stanleyi* with 5.2% of counts (mean = 19 ± 3.8) (Supplementary Table 3.1. see in Appendix).

The Chao 1 estimator indicated that 82-90% of the estimated species richness present in the study sites was recorded, with similar proportions of species detected near (Observed richness = 26, Chao1 = 29 ± 3.9 [mean ± SD]; 95% confidence intervals [CI] = 27-31) and far from the road (Observed richness = 25, Chao 1 = 31 ± 5.2; 95% CI = 28-33). Estimated species richness did not differ between transects near and far from the road ($F_{1,16}$ = 0.01, P = 0.91).

The change in abundance of the four bird habitat groups with distance from the road was not significant (Full model: $F_{3,14}$ = 2.5, P = 0.091). However, the abundance of shrubby páramo specialist species was significantly higher far from the road than near the road ($F_{1,16}$ = 11.5, P = 0.003), whereas abundance did not differ for páramo species ($F_{1,16}$ = 2.5, P = 0.13), *Polylepis* forest species ($F_{1,16}$ = 1.3, P = 0.29), or generalist species ($F_{1,16}$ = 0.3, P = 0.62; Fig.1).

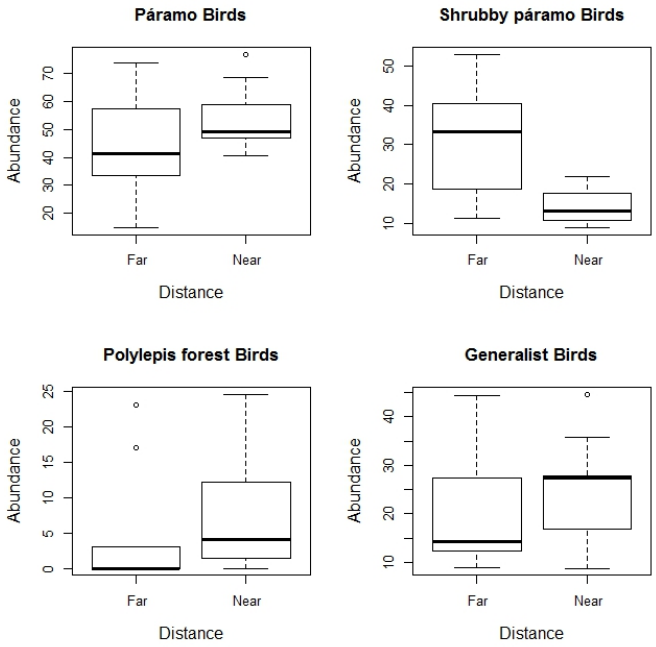

Figure 1. Abundance variation of bird habitat group detected at two distances from road (near ~ 25 m, far ~ 250m) in Cajas National Park, Ecuador. All paired comparisons were not significantly different except for shrubby páramo specialist.

The abundance of the three most abundant species was significantly influenced by distance from the road (Full model: $F_{2,14}$ = 5.9, P = 0.008). C. fuscus ($F_{1,16}$ = 8.5, P = 0.012) was more abundant near the road, *A. flammulata* was more abundant far from the road ($F_{1,16}$ = 20.8, P < 0.001) and the abundance of *P. unicolor* did not differ with distance from the road ($F_{1,16}$ = 2.34, P = 0.14; Fig. 2).

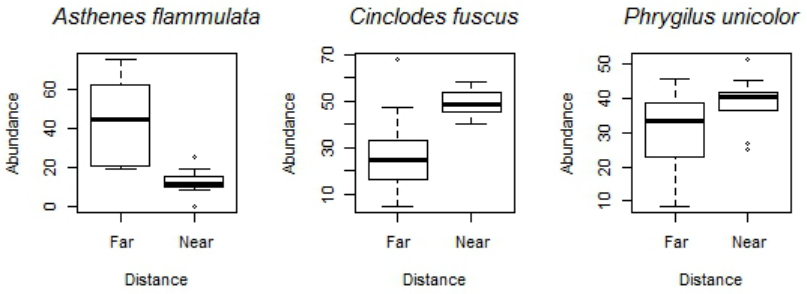

Figure 2. Abundance variation of the three most abundant bird species detected at two distances (near ~ 25 m, far ~ 250 m) in Cajas National Park, Ecuador. All paired comparisons were significantly different except for *Phrygilus unicolor*.

Community ordination

The NMDS of the bird habitat groups enabled us to plot transects and predictors in two-dimensional species space. Distance to the road significantly influenced the composition of bird habitat groups (stress = 12.15, R^2 = 0.23, P = 0.01). Páramo birds were grouped in the top (near the road), shrubby páramo birds on the right (far from the road) and *Polylepis* forest birds on the bottom left of the ordination (Fig. 3). Further, the vegetation component PCI (R^2 = 0.55, P = 0.003) significantly explained changes in the composition of bird habitat groups: Generalist and páramo birds increased along a gradient of increasing PCI reflecting a change from páramo grassland to increasing proportion of non-native plants. Shrubby páramo birds were located on the opposite side of the PCI gradient and thus located at PCI values depicting páramo grassland cover with decreasing proportion of non-native plants (Fig. 3). PCII (R^2 = 0.30, P = 0.07) did not significantly explained the changes among habitat groups.

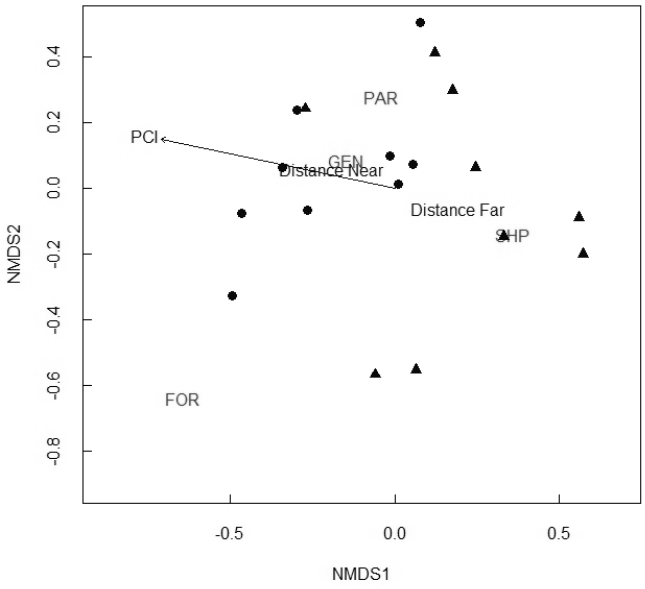

Figure 3. Non-metric multidimensional scaling (NMDS) biplot of bird habitat groups detected along 18 strip transects in Cajas National Park, Ecuador. The filled triangles are the nine transects located far from the road (~ 250 m) and the filled circles are nine transects near from the road (~ 25 m). The arrow points along the gradient of increasing non-native plant species and from low to high vegetation cover (habitat component PCI). The habitat preferences codes are: PAR, páramo specialist; SHP, shrubby páramo specialist; FOR, *Polylepis* forest specialist; and GEN, generalist.

Discussion

Bird species richness was not affected by proximity to the road. However, we did detect differences in the abundance of specific bird habitat groups between transects near and far from the road with shrubby páramo species being more abundant far from the road. Such changes were also reflected in slight differences in the composition of bird habitat groups between transects near and far from the road.

Richness, abundance and community structure

Species richness of birds was similar along transects near and far from the road. This result was unexpected given the large number of studies reporting reduced species richness near roads (e.g., Forman and Alexander 1998; Fahrig and Rytwinski 2009). Certainly, several studies have reported that high levels of species richness are not always associated with natural habitats, but rather with distinct ecological differences in the habitat (Camp and Best 1993; Clergeau et al. 1998). However, while species richness may be similar, there may be differences in abundance and composition of the specific bird groups due to habitat and vegetation changes (Laurance 2004).

Even though we did not find significant differences in the abundance of any habitat group with distance to the road, the abundance of shrubby páramo specialist species increased with distance from the road. This pattern was particularly driven by *A. flammulata*, which represented 52% of shrubby páramo detections. This species and also other shrubby páramo specialists are strongly associated with these native shrubs and bushes in páramo grassland (Tinoco and Astudillo 2007), probably because of their inflorescences attracting insects (P. X. Astudillo, pers. obs). Quite in contrast and unexpectedly, we found that *C. fuscus*, a páramo specialist, showed significantly higher abundance near the road. However, a higher abundance of single, even specialized páramo species, along roadsides is not always associated with high quality habitats (Forman and Alexander 1998; Camp and Best 1994) as roads are linked to high levels of predation, parasitism and mortality (Reijnen and Foppen 1994; Ortega and Capen 1999; Forman and Alexander 1998).

Most importantly, our community analyses (NMDS) suggested that changes in composition of bird habitat groups with respect to proximity to the road may be related to changes in vegetation cover, i.e. the increasing proportion of non-native plant species

within páramo grasslands near roads (gradient of PCI). The biplot associated shrubby páramo species with transects located far from the road. This result was again particularly influenced by the highly abundant species *A. flammulata* which is strongly associated with shrubs and bushes in páramo grassland (Tinoco and Astudillo 2007) occurring particularly along transects far from the road while the vegetation near the road was characterized by an increase of non-native plants, especially *P. racemosa*. We suspect that the Cuenca-Molletura-Naranjal road in Cajas National Park has facilitated the spread of this non-native species within the park and that its presence has modified the local vegetation by decreasing the availability of natural páramo grassland and consequently affecting the composition of bird habitat groups. This adds to previous studies showing that clear changes in the vegetation structure and composition near roads strongly modify bird communities (Beissinger and Osborne 1982; Forman and Alexander 1998) with habitat-specialized birds exhibiting avoidance of roads (Forman and Alexander 1998; Forman 2000; Laurance 2004). Also in our study we found generalists such as *Turdus fuscater* and *Zonotrichia capensis* species typically associated with disturbed vegetation and urban areas in the modified páramo habitat near roads (Ridgely and Greenfield 2001; Tinoco and Astudillo 2007). Thus, the presence of the non-native *P. racemosa* at roadsides may particularly influence the bird community composition by attracting *Polylepis* forest species, which also seem to find alternative perching and nesting space near roads. These findings are in accordance with studies showing that habitat changes in terms of high numbers of non-native plant species along roadsides influence the avifaunal composition (Forman and Alexander 1998) with a few dominating generalists being attracted by this new conditions (Camp and Best 1993; Clergeau et al. 1998).

In summary, our findings suggest that the presence of the road does influence the avifauna in Cajas National Park by altering the abundance and particularly the

composition of bird species. Decreasing numbers of shrubby páramo species and increasing numbers of a single páramo specialist and many generalist species near roads highlight the fact that species richness alone is not a suitable measure to evaluate the impact of the road on the avifauna in Cajas National Park. More importantly, our findings suggest that the main driver for these differences in bird community composition is an overall change in habitat from native shrubs dominating far from the road to the planted non-indigenous *Polylepis* species prevailing the roadside. These findings underscore the importance of assessing the responses of complete communities to detect whether specific groups or specialized species are more sensitive than others and can thus be used as indicators for habitat modification. Furthermore, we recommend that park managers monitor the spread of this non-indigenous plant as it may have important implications for the composition of birds within the park as a whole.

3 Identifying the relative importance of forest patch characteristics for bird guilds: a landscape-wide network approach

With Ingo Grass, Edwin Zárate and Nina Farwig

3 – Identifying the relative importance of forest patch characteristics

Abstract

In an increasingly human-modified world, a better understanding of associations between fragmented habitats and species in mosaic landscapes becomes increasingly important. So far, these associations have been mostly investigated based on correlations and in an isolated, patch-by-patch manner. Yet, mobile taxa often use and connect multiple habitat patches, resulting in habitat-species networks. Here, we studied networks composed of *Polylepis* forest patches and three habitat guilds of birds (i.e. *Polylepis* specialists, páramo specialists, and generalist birds that use both *Polylepis* and páramo habitats) in the high-altitude Andes of Ecuador. We used the centrality of *Polylepis* patches within these networks as a measure of their relative importance for birds within a given guild. Patch centrality differed considerably depending on guilds and patch characteristics. For *Polylepis* specialists, patch centrality decreased with larger and more irregular shaped patches, but increased with higher altitude. In contrast, patch centrality for generalist birds was positively related to patch area and shape irregularity, but not to patch altitude. Increasing influence of the surrounding páramo vegetation reduced the patch centrality for both *Polylepis* specialists and generalist birds. Patch centrality for páramo specialists was not related to the recorded patch characteristics. In conclusion, the importance of forest patches for *Polylepis* specialists in our study area is driven by characteristics related to the quality but not the quantity of available habitat, whereas forest generalists depend on larger *Polylepis* patches and positively respond to edge effects. A network approach facilitates identifying those patches that are crucial contributors to the overall structure of the habitat-species network on a landscape scale. Thus, network theory is a promising tool to aid conservation and landscape planning in mosaic landscapes.

3 – Identifying the relative importance of forest patch characteristics

Introduction

The ongoing fragmentation and modification of natural ecosystems increasingly confine biodiversity to human-shaped mosaic landscapes (Foley et al. 2005; Laurance et al. 2013). A better understanding of biodiversity patterns in these landscapes is therefore critical for ecology and conservation (Gardner et al. 2009). In forest landscapes, birds are considered valuable indicators of the health of fragmented forest patches, as their distribution and community composition is usually strongly linked to the quantity (e.g., patch area) or quality (e.g., plant composition) of forest habitat (Moonen and Bàrberi 2008). Moreover, birds provide essential ecosystem functions to forests, such as pollination, seed dispersal or pest control (Sekercioglu 2006).

Most studies that investigate role of forest patch quantity or quality for birds focus on correlations between patch characteristics and measures of bird diversity (Neuschulz et al. 2011; Berens et al. 2014). Thereby, these correlations are investigated in an isolated, patch-by-patch manner, which, however, can be of limited value when the focus is on landscape-wide associations or conservation planning. Particularly for birds, forest patches do not exceed isolated effects; instead, they are in many cases perceived as a connected network of habitat that is temporarily or permanently used for nesting, foraging, or as stepping-stones across the landscape (Verboom et al. 2001; Neuschulz et al. 2013). Thus, a network approach advances our understanding on how bird communities depend on forest patches in mosaic landscapes.

Recently, centrality indices have gained popularity to identify specific nodes in networks that are important connectors of network structure and that further mediate interactions to more peripheral nodes in communities (Girvan and Newman 2002; Jordán et al. 2007). For example, Google$^{TM's}$ PageRank^{TM} algorithm builds up on centrality

measures to identify those webpages that are assigned the highest priority in web searches (Bryan and Leise 2006). Gómez et al. (2013) focused on the centrality of primate species within a primate-parasite network to identify new pathways for emerging infectious diseases to humans. With respect to birds, Rodríguez-Pérez et al. (2014) investigated avian seed dispersal in a spatially-explicit network approach, with fruiting trees as nodes and expected bird movements as edges of this network. The authors showed that the spatial distribution, abundance and species identity of fruit crop drive seed dispersal in their study landscape, and that birds are strong drivers of landscape connectivity.

Expecting a similar functional connectivity in mosaic landscapes, forest patches and bird species are either directly connected (when one or more species occupy a given patch) or indirectly connected (when two or more patches are connected by one or more species that share these patches). The result is a network composed of closely connected and more peripheral forest patches. Here, we suggest that centrality measures can be used to identify those patches that are crucial to the overall structure of the forest patch-bird networks, and thus bird persistence on a landscape scale. The centrality of forest patches will likely depend on bird species-specific preferences with respect to patch quantity or quality. Assigning birds into different habitat guilds (e.g., forest specialists, generalists and grassland species; Grass et al. 2014) should therefore benefit the detection of forest patch-bird associations.

In the high Andes of South America, *Polylepis* woodlands occur as mosaic landscapes that consist of *Polylepis* forest patches interspersed by páramo grassland. *Polylepis* woodlands are a naturally fragmented ecotype; however, their current distribution is also shaped and threatened by human activities such as fires to promote grazing, deforestation, and firewood collection (Purcell and Brelsford 2004; Gareca et al. 2010). At the same time, *Polylepis* woodlands are crucial for the conservation of globally

threatened bird species (Benham et al. 2011). Their mosaic character, ongoing human threat, and importance to birds make *Polylepis* woodlands ideally suited as a model system to unravel how bird communities depend on forest patches in human-shaped mosaic landscapes using a network approach. In this study, we used information on patch characteristics of *Polylepis* forest (e.g., area and plant composition) to relate these to their relative importance for three different bird guilds (*Polylepis* forest specialists, generalist species and páramo grassland specialists) in an Andean landscape in Ecuador. In doing so, we applied a network approach based on the distribution of bird guilds across *Polylepis* patches, and used centrality measures of *Polylepis* patches within these forest patch-bird guild networks as an estimate of their relative importance for bird guilds on a landscape scale.

Material and methods

Study area and design

Fieldwork was done in Cajas National Park in the southwestern Andes of Ecuador (2°51'S, 79°11'W). The park covers an area of 28,544 ha, with an elevation range of 3,160 m to 4,445 m (Delgado et al. 2006). Mean annual precipitation was 1,200 mm and monthly temperatures ranged from 0–20°C (IERSE 2004). The park consists of 90 % páramo grassland that is interspersed by small patches of *Polylepis* woodland, with forest patches of varying sizes (< 1.0 ha–44 ha) throughout the páramo landscape (Minga and Verdugo 2007).

We selected 15 patches of *Polylepis* forest that ranged from 1.65 ha to 17.36 ha in size (7.25 ha ± 5.16 ha; mean ± SD; Supplementary Figure 3.1. see in Appendix) and from 3,549 m to 4,029 in altitude. We considered a patch as continuous forest that was separated by at least 150 m from the next closest patch. We chose this distance as the

boundaries of *Polylepis* patches are often not clearly defined (e.g., isolated *Polylepis* trees and shrubs often occur within 150 m distance of given patch). The distance of the 15 patches to the nearest other *Polylepis* patch ranged from 154 m to 707 m (347 m ± 195 m). Pairwise distances between study sites ranged from 314 m to 17,192 m (6,510 m ± 5,165 m). In addition to patch area, we assessed the perimeter of each forest patch and used this information to calculate a shape index that quantified the deviation of forest patches from a perfect circle:

$$Shape = \frac{P}{2\sqrt{\pi A}}$$

where P represents the perimeter of a given patch (m) and A is the area of patch (m^2). The index approaches 1 for a circular patch and increases as the shape becomes more irregular. The shape index was highly correlated to forest area ($r = 0.85$, $P < 0.001$). To obtain a shape component independent from patch area, we calculated a linear regression with area as predictor, and in the following refer to the model residuals as 'patch shape'.

Bird census

Inside each *Polylepis* patch, we installed four point counts that were separated by at least 150 m to avoid double counting. Within each point count, we recorded all birds heard or seen within a 25 m radius within 15 min observation, excluding flyovers. Point counts were done three times within August 2012–April 2013 and another three times within August 2013–April 2014. Species were identified following Ridgely and Greenfield (2001) and Tinoco and Astudillo (2007). Afterwards, each species was assigned to one of three habitat guilds: 1) *Polylepis* forest specialists that only occur in *Polylepis* woodland; 2) generalists that make use of both *Polylepis* forest and páramo habitats; and 3) páramo specialists that only occur in páramo habitats.

Within-forest patch characteristics

At each of the point counts we established a circular plot with 12 m radius within which we installed four 12 m transects radiating out in the cardinal directions from the plot center. In each circular plot we counted and identified all tree and shrub individuals with ≥ 3 cm diameter at breast height (DBH). Similarly, we counted and identified all woody-shrubs with < 3 cm DBH that were touched when walking along the transects with arms extended. With the exception of a few species (i.e., plants from the genera *Gynoxis*, *Pentacalia*, *Valeriana*) all shrubs and trees were identified to species level. The plant diversity per study site was calculated as the Shannon diversity over all counted tree and shrub individuals. In addition, we estimated canopy cover in five classes every 3 m along each transect (12 measures per plot in total; 0= 0–19%; 1= 20–39%; 2= 40–59%; 3= 60–79%; 4= 80–100%) and averaged these values for each study site. At the same locations, the vertical vegetation profile was estimated, using a 3 m pole marked at 0.5 m intervals where each interval was counted as having contact with a plant or not; above 3 m, the vegetation profile was estimated at 1 m intervals Using these information we calculated the Shannon diversity of the vertical vegetation profile for each location within a given plot and averaged values for each study site.

Polylepis forest patches can differ considerably in plant composition. For example, páramo plants are often growing within *Polylepis* patches (Minga and Verdugo 2007). To account for compositional differences we estimated the proportional cover of three vegetation types within each circular plot: 1) woody *Polylepis* forest plants that are restricted to *Polylepis* forest and include *Polylepis reticulata* and *Polylepis incana*; 2) woody native páramo plants that are typically distributed in the páramo and include the genera *Hesperomeles* (Rosaceae), *Chuquiraga* and *Diplostephium* (Asteraceae); and 3) cosmopolitan woody native plants that occur in both *Polylepis* patches and páramo and

include the genera *Gynoxis* (Asteraceae), *Braychyotum* and *Miconia* (Melastomataceae). for the site-environment matrix and other characteristics of study sites (Supplementary Table 3.1. see in Appendix).

We then performed a principal component analysis (PCA) on the correlation matrix of the within-forest patch characteristics of each study site to retain principal components (PC) that we used for our statistical models. Based on screeplots and the broken-stick method we selected the two first principal components (68.4% total variance explained) for further analyses (Jackson 1993). The first component (PCI= 39.6%) reflected a change to a less diverse vegetation profile, loss in canopy cover and increasing DBH and a higher proportion of woody native páramo plants. The second component (PCII= 28.8%) reflected a change to a more diverse vegetation profile and increasing influence of cosmopolitan woody native plants (Supplementary Table 3.2. see in Appendix). We therefore considered PCI to represent increasing influence of the surrounding páramo matrix on forest patches, while PCII represented a change towards more heterogeneous and vertically complex forest patches with influences from both *Polylepis* and páramo vegetation types.

Network and statistical analyses

For each of the three bird guilds, we built a quantitative, bipartite forest patch-bird species network. These networks were topologically similar to other quantitative ecological networks. However, instead of interactions between trophic groups, we used abundance information of bird species in a given forest patch as interaction frequency. Our networks therefore did not measure “interactions” of a given bird species with a forest patch *sensu stricto* (e.g. foraging on fleshy-fruited plants, or movements between patches). Instead, they represented a topological view on the contribution of each forest patch to the structure of the regional bird community within a given guild. The bipartite networks

were then converted to weighted unipartite representations, where forest patches are connected to another via shared bird species, with bird abundances as weights. The relative importance of specific nodes (i.e. forest patches) within each network can be quantified using different network indices. We calculated four widely-used centrality indices as measures of node importance: 1) unweighted degree, i.e. bird richness of forest patches; 2) Opsahl degree, a weighted measure of species degree, which also integrates interaction frequencies between nodes; 3) weighted closeness centrality, which captures patterns of indirect sharing of bird species across the entire network; and 4) eigenvector centrality, a more direct measure of sharing between nodes as centrality of forest patches increases given that other forest patches that are closely connected also have high eigenvector centrality, and *vice versa*. See Gómez et al. (2013) as well as references therein for more exhaustive descriptions of the four centrality indices used in our study.

Following Gómez et al. (2013), we then calculated a composite index that integrated the different complementary and redundant components of the four above-described centrality indices by calculating a PCA on the specific indices for each of the three bird guilds (Supplementary Table 3.3. see in Appendix). We then used the first principal component of a given PCA as the composite centrality index. For each of the three bird guilds, the four centrality indices were in all cases negatively correlated to a given composite index, implying that increasing composite indices reflected a decrease in the centrality of forest patches in the three patch-bird guild networks (Supplementary Table 3.3 see in Appendix). To ease interpretation, we multiplied the three composite indices with −1, so that higher values indicated higher centrality. In the following we refer to the composite index of *Polylepis* patches for each respective patch-bird guild network as “patch centrality”.

3 – Identifying the relative importance of forest patch characteristics

We used multiple linear regression models (LMs) to relate the variation in patch centrality for each bird guild to patch area (ln-transformed), patch shape, altitude, páramo influence (PCI), and patch heterogeneity (PCII). Inspection of model residuals in 1,500 m distance indicated spatial autocorrelation in some classes, thus violating test assumptions of independence of residuals (Supplementary Figure 3.2. see in Appendix). We therefore decided to use spatial simultaneous autoregressive error model estimations (SARs) that incorporate spatial information (easting and northing of study sites) into models. Given spatial autocorrelation of residuals, SARs are generally regarded as more robust than LMs and often strengthen conclusions from statistical inference (Lichstein et al 2002; Dormann et al. 2007). Inspection of model residuals indicated better performance of SARs in contrast to LMs excluding spatial structure (Supplementary Figure 3.2. see in Appendix).

To verify that our measure of patch centrality differed from more classical methods that can be used to assess the relative importance of forest patches for bird guilds, we further ran SARs using species richness and Shannon diversity of bird guilds of each patch as dependent variables (richness and diversity of páramo specialists were sqrt-transformed). We found substantial differences to results based on centrality measures, which indicated that many effects of patch characteristics remain undetected when solely focusing on bird richness or diversity (Supplementary Table 3.4. see in Appendix).

Results

Centrality of *Polylepis* patches in each forest patch-bird guild network differed considerable among guilds and with respect to patch characteristics (Supplementary Figure 3.1. see in Appendix). For *Polylepis* specialists, centrality of forest patches decreased as patch area and shape irregularity increased (Table 1). In contrast, centrality based on the same patch characteristics increased for forest generalists, whereas centrality of patches for páramo specialists was neither related to patch area nor shape (Table 1). Altitude of forest patches increased centrality for *Polylepis* specialists only (Table 1). Structural changes associated with PCI (i.e., increasing influence of the surrounding páramo matrix) reduced centrality of forest patches for both *Polylepis* specialists and forest generalists, but not for páramo specialists (Table 1). Changes in patch characteristics associated with PCII (i.e., increases in patch heterogeneity with influences from both *Polylepis* and páramo vegetation types) reduced centrality of patches for *Polylepis* specialists, but did not affect patch centrality for forest generalists or páramo specialists (Table 1).

3 – Identifying the relative importance of forest patch characteristics

Table 1. Patch characteristics of fragmented *Polylepis* forest determine their centrality within landscape-wide forest patch-bird guilds networks. Networks were studied for three habitat guilds: *Polylepis* forest specialist, forest generalists and páramo specialists. Shown are effects of area, shape irregularity and altitudinal position of *Polylepis* patches as well as of two principal components derived from PCA on vegetative diversity and composition of forest patches (PCI: increasing influence of the surrounding páramo matrix; PCII: increases in patch heterogeneity with influences from both *Polylepis* and páramo vegetation types). Significant effect ($P < 0.05$) are highlighted in boldface type

	***Polylepis* specialists**				**Generalists**				**Páramo specialists**			
	Estimate	SE	*Z*	*P*	Estimate	SE	*Z*	*P*	Estimate	SE	*Z*	*P*
Intercept	0.004	0.107	0.037	0.971	−0.082	0.154	−0.532	0.595	−0.572	1.194	−0.479	0.632
Area	**−0.650**	**0.178**	**−3.651**	**< 0.001**	**0.561**	**0.246**	**2.279**	**0.023**	3.271	1.956	1.673	0.094
Shape	**−0.794**	**0.226**	**−3.512**	**< 0.001**	**0.718**	**0.313**	**2.296**	**0.022**	0.260	2.482	0.105	0.917
Altitude	**0.884**	**0.229**	**3.862**	**< 0.001**	0.160	0.309	0.518	0.604	3.806	2.481	1.534	0.125
PCI	**−1.537**	**0.148**	**−10.357**	**< 0.001**	**−0.593**	**0.208**	**−2.847**	**0.004**	−2.731	1.642	−1.663	0.096
PCII	**−1.059**	**0.280**	**−3.777**	**< 0.001**	−0.470	0.382	−1.230	0.219	1.727	3.054	0.565	0.572

Discussion

Using a network approach, we found that the relative importance of *Polylepis* forest patches for an Andean bird community, as measured by their centrality within forest patch-bird guild networks, strongly differed with respect to patch characteristics. Whereas increasing patch area and shape irregularity were negatively related to patch centrality for *Polylepis* forest specialist birds, patches with these characteristics had high importance for forest generalists. Similarly, patch centrality increased with patch altitude for *Polylepis* specialists, but not for forest generalists. High influence of the surrounding páramo matrix on the vegetative profile and composition of *Polylepis* patches reduced patch centrality for both *Polylepis* specialists and forest generalists but not for páramo specialists. In fact, patch centrality for páramo specialists as only weakly related towards *Polylepis* patch characteristics, indicative of their stronger association with the quality of the páramo matrix surrounding *Polylepis* patches. Our study shows that a network approach is a suitable tool to understand the relative importance of habitats with different quantity and quality in human-shaped mosaic landscapes.

Guild-specific differences in patch centrality

The centrality measures revealed strong differences in the responses of the habitat guilds to patch characteristics. The most important forest patches for *Polylepis* specialists had regular shapes (and hence weak edge effects), low influence of the surrounding páramo matrix (PCI and PCII) and were mostly found in higher altitudes. These findings corroborate that *Polylepis* specialists strongly avoid forest edges and depend on high-quality forest patches with a unique vegetation composition (Cahill and Matthysen 2007; Tinoco et al. 2013). In fact, the quality of *Polylepis* patches in our study area was more important than their quantity, as increasing patch area was negatively related to patch centrality of *Polylepis* specialists. *Polylepis* specialists have been shown to maintain high

abundances in small and isolated *Polylepis* patches (Fjeldså 1993). The conservation of high-quality *Polylepis* patches thus should become a conservation priority (see also Fjeldså 1993). Thereby, a high density of large *Polylepis* trees and dense vegetation cover can be particularly beneficial (Lloyd 2008b).

Contrasting the decrease in patch centrality with patch area for *Polylepis* specialists we found a positive relationship for forest generalists. A previous study in our study area reported positive bird richness-patch area relationship (Tinoco et al. 2013). However, as the authors point out themselves, the relationship between the size of *Polylepis* patches and bird richness or abundance contrasts among species and studies (Fjeldså 1993; Lloyd 2008a; Tinoco et al. 2013). Although arguably being a simplification, assigning bird species into habitat guilds therefore helps untangling the underlying species-specific responses. Higher irregularity in patch shape positively influenced patch centrality for forest generalists. Irregular shapes result in stronger edge effects, which can benefit forest generalists that are able to withstand edge effects that often deter forest specialists (Grass et al. 2014). Correspondingly, whereas *Polylepis* specialists depended on high-quality forest patches, centrality of forest patches for forest generalists was more related to patch quantity. As altitude did not predict patch centrality, forest generalists also occupied a wider altitudinal distribution within the 3,500 m and 4,000 m range than *Polylepis* specialists, which is likely the result of their higher flexibility in the use of *Polylepis* and páramo habitats.

As might be expected not patch characteristics of the *Polylepis* patches but rather the quality of the surrounding matrix seemed to be important for páramo specialists. Important páramo features include the availability of bunch grasses, cushion bogs, or native woody bushes and shrubs, but also exotic tree species. (Minga and Verdugo 2007; Astudillo et al. 2014). Future studies could use a similar network approach as ours to

investigate how their distribution in the páramo landscape relates to páramo specialists on a landscape scale.

Future directions

Here we applied a network approach to investigate shifts in the centrality, and hence the relative importance, of fragmented forest patches distinguished by different patch characteristics for bird guilds in an Ecuadorian mosaic landscape. We suggest that our approach has several merits over other, more classical metrics and methods. First, it considers these associations not on a local but on a landscape scale, and thus may be a better fit to the overall perception of mosaic landscapes by mobile taxa such as birds. Second, our network approach strongly reflects the functional contribution of birds to landscape connectivity (e.g., Rodríguez-Pérez et al. 2014). We consider this study as a first step to show the applicability and merits of our approach for understanding biodiversity patterns in human-shaped landscapes. It may be readily used to guide conservation decisions in various other mosaic landscapes, also including non-forest ecosystems, such as fragmented grasslands or riverine systems. Linking habitat-species networks to data on animal movement or relating centrality measures of habitat patches to ecological processes (e.g. pollination or seed dispersal of plants), will advance our understanding on biodiversity patterns and ecosystem processes in natural and human-shaped mosaic landscapes.

4 Matrix heterogeneity enhances bird movement in a fragmented High-Andes landscape

With Dana G. Berens, David C. Siddons and Nina Farwig

4 – Matrix heterogeneity enhances bird movement

Abstract

Habitat fragmentation is one of the most important challenges for conservation today. Many studies have shown that heterogeneous matrices increase overall landscape complexity and promote connectivity between habitat fragments. However, to what extent this complexity influences species movement of different habitat guilds in Andean region is little understood. In an Ecuadorian páramo, we studied the relationship between bird habitat guild movements, *Polylepis* forest patch characteristics and surrounding páramo matrix heterogeneity. Overall, we detected 318 individuals of 25 bird species making patch-matrix movements. The number of species moving, the number of *Polylepis* specialists and the similarity of species recorded in the patch and surrounding matrix were positively related to the complexity of the páramo matrix. Our findings suggest the vital role of páramo heterogeneity to enhance connectivity among fragmented *Polylepis* woodland, especially for *Polylepis* specialist birds. We emphasize that the high-altitude Andes show, besides the *Polylepis* patches, a gradient of habitats where the páramo matrix it is also important to quantify for conservation on landscape scale

Introduction

One of the major threats in conservation biology is the increasing habitat loss and forest fragmentation with consequent negative effects on species numbers and community composition (Sala et al. 2000; Fahrig 2013). Loss of native vegetation, for example forests, leads to reduction of available forest, which in many cases is replaced by grassland (Sala et al. 2000; Fischer and Lindenmayer 2007). The remaining forest patches are not only reduced in size but are also increasingly isolated. Smaller patches generally support less species (Robinson and Sherry 2012; Fahrig 2013) and greater isolation inhibits animal movements between patches (Johnson et al. 1992; Fahrig 2013). Connectivity across fragmented landscapes could mitigate some of these problems.

Enhanced connectivity has been shown to depend not only on the vegetation structure and composition of a patch in itself, but also that of the surrounding matrix (Baum et al. 2004; Vergara et al. 2013). A Heterogeneous matrix has been shown to be crucial for biodiversity and may provide diverse resources for species (Tews et al. 2004; Watson et al. 2014).

These general patterns have been shown for bird species in numerous studies (Leck 1979; Sodhi et al. 2004; Latta et al. 2011). It is known that bird species in a fragmented landscape can be influenced by patch size (Fischer and Lindenmayer 2007; Fahrig 2013), the degree of patch isolation (i.e. nearest patch distance), and matrix configuration (Fischer and Lindenmayer 2007; Mulwa et al. 2012; Neuschulz et al. 2013). Studies have shown that, for example, bird species richness in fragmented habitats increases with woody surrounding matrices of forest fragments (Mulwa et al. 2012). Birds also use these types of matrices as movement corridors (Robichaud et al. 2002, Vergara et al. 2013), which is also reflected in shared species between the patch and the matrix (Kattan et al. 2006).

Different bird habitat guilds respond differently to habitat fragmentation (Tews et al. 2004; Lloyd and Marsden 2011; Neuschulz et al. 2013). Forest-specialist birds, for example, show few movements over greater habitat modification (Lloyd and Marsden 2011; Neuschulz et al. 2013; Vergara et al. 2013), although increasing natural habitat heterogeneity in matrices promote more bird movements even of this specialized guild (Tews et al. 2004). This knowledge could be crucial for management and conservation of fragmented landscapes.

Páramo grassland ecosystem is naturally a very heterogeneous habitat with a high proportion of woody native plants (Neill 1999; Baquero et al. 2004; Minga and Verdugo

2007; Gareca et al. 2010) and it supports high-altitude *Polylepis* (Rosaceae) woodland patchily distributed throughout (Gareca et al. 2010; Herzog et al. 2012). This ecosystem is an important center for bird diversity and endemism in the region (Stattersfield et al. 1998; Ridgely and Greenfield 2001; BirdLife International 2004). Beyond, habitat loss in the páramo grassland is widespread, and remnants of natural areas are under pressure from human activities such as burning and grazing (Sierra 1999; Hofstede et al. 2002; Mena-Vásconez and Hofstede 2006), which are postulated reasons for the strongly fragmented configuration of *Polylepis* patches. Several bird species are highly dependent on *Polylepis* forest patches as well as the surrounding páramo grassland (Fjeldså and Krabbe 1990; Ridgely and Greenfield 2001; Tinoco and Astudillo 2007; Lloyd and Marsden 2008). Thus, more complex páramo grassland between *Polylepis* forest patches may be an important factor for promoting connectivity across the landscape.

For this reason we aim to explore how the area of the *Polylepis* patches, nearest patch distance and the complexity of the páramo matrix (i.e. higher proportion of woody plants) influence species richness and abundance of bird movements between *Polylepis* forest patches and the páramo matrix. We also used bird counts in both the patch and matrix to assess community similarity. We expected a higher number of movements by forest specialists between patches with complex surrounding matrices as well as between large and close patches. We also expected greater species similarity between complex páramo matrices and the associated *Polylepis* patches.

Materials and Methods

Study area and design

We carried out this study in Cajas National Park (2°51’S, 79°11’W) in the southwestern Andes of Ecuador. The park covers 28,544 ha with an elevation range between 3,100 m to

4,445 m (Delgado et al. 2006). The temperature ranges from 0-20°C (IERSE 2004) and mean annual rainfall is between 1,000 and 1,400 mm with the highest rainfall in March and April and the lowest in August (IERSE 2004; Celleri et al. 2007).

The park consists of 90% páramo grassland matrix with *Polylepis* woodland fragments of varying sizes (<1.0–44 ha) dominated by two native *Polylepis* species (*P. incana* and *P. reticulata*; Minga and Verdugo 2007). The páramo matrix vegetation is dominated by native grassland combined with cushion páramo plants as well as woody native shrubs and bushes with a high vegetation profile. (Baquero et al. 2004; Minga and Verdugo 2007)

We selected 15 localities at elevations between 3,550 to 4,030 m, each associated with a single *Polylepis* patch and its respective matrix within Cajas National Park (Supplementary Figure 4.1. see in Appendix). We defined a patch as a continuous woodland area separated by at least 150 m from the next patch. Patch area ranged from1.65 ha to 17.36 ha (7.25 ha ± 5.16 ha [mean ± SD]) and nearest patch distance ranged from 154 m to 707 m (347 m ± 195 m; Supplementary Table 4.1. see in Appendix). The patch area and nearest patch distance were calculated using GIS software (ArcGis 9.1) based on 1:5000-scale orthophoto provided by GIS department of Cajas National Park and field improves via GPS.

We sampled the vegetation structure of surrounding páramo grassland by installing four circular plots in each bird census transect (described below) with the center of each plot separated by at least 50 m. In each circular plot we established four transects (12 m long) oriented in the cardinal directions. Every three meters the foliage height profile was estimated using a 3 m pole marked at 0.5 m intervals where each interval was counted as having contact with the vegetation or not. Beyond 3 m, the profile was estimated at 1 m

intervals to the top of the canopy. We counted and identified all shrubs (≤ 3 cm diameter at breast height [DBH]) that were touched by an observer walking with arms extended along each transect and all trees (> 3 cm DBH) present in the circular plot. While the majority of plants were identified to species level, a few taxonomically difficult plants (i.e. genera *Gynoxys*, *Pentacalia*, *Valeriana*; Ulloa et al. 2004) could only be identified to genus level.

To account for the variability of páramo grassland, we estimated the percentage cover of seven habitat types within each circular plot: 1) *Polylepis* forest plants, which are trees restricted to *Polylepis* forest and include the native species *Polylepis reticulata* and *P. incana* (Minga and Verdugo 2007); 2) native páramo woody plants, a habitat type typically distributed in the páramo matrix and including the genera *Chuquiraga*, *Diplostephium* (Asteraceae), and *Hesperomeles* (Rosaceae; Minga and Verdugo 2007; Minga et al. 2013); 3) cosmopolitan woody plants, widely distributed native plants that are found in both *Polylepis* forest and the páramo matrix, characterized by the genera *Brachyotum*, *Miconia* (Melastomataceae), and *Gynoxys* (Asteraceae; Minga and Verdugo 2007); 4) cushion páramo, an open habitat dominated by cushion plants such as *Plantago rigida* and *Oreobous ecuadorensis* (Minga and Verdugo 2007; Minga et al. 2013); 5) páramo grassland, an open habitat dominated by bunch-grass species of the genera *Chalamagrostis* (Minga and Verdugo 2007; Minga et al. 2013); 6) water bodies such as ponds and streams; and finally 7) rocky substrates, which are naturally present within the study area.

We characterized the páramo matrix for each locality by calculating a Shannon index for plant diversity using the shrubs and tree counts and a Shannon index for vertical complexity using the touches of the foliage height profile. We condensed the description of the páramo matrix via principal component analysis (PCA) based on the average

proportion of the seven habitat types in the four circular plots plus the Shannon indices for plant diversity and vertical complexity (Supplmentary Table 4.1. see in Appendix). The first component of the PCA (PCI) explained 35.27% of the variance and reflected a change in the páramo matrix from low proportion of páramo grassland and cushion páramo to increased proportion of native woody plants and cosmopolitan woody plants with a more vertically complex vegetation. The second component (PCII) explained 20.56% of the variance and reflected a change in the páramo matrix to an increasing proportion of páramo grassland with less cushion páramo cover. Therefore, we considered PCI to represent an increasingly heterogeneous páramo matrix with high influence of woody plants (native páramo and cosmopolitan), whereas PCII represented a more homogenous páramo matrix with a high proportion of páramo grassland (Supplementary Table 4.2. see in Appendix). As PCI represents increasing matrix heterogeneity, we only retained PCI for the analyses.

Bird census

All bird censuses were conducted from August 2012 to April 2014 in two consecutive years with three repetitions per year. We chose eight months campaigns to sample over the various seasonal rainfalls (Celleri et al. 2007). All bird surveys started 15 minutes after sunrise and the order they were performed in was random. We used the field guides of Ridgely and Greenfield (2001) and Tinoco and Astudillo (2007) for bird identification and to assign one of three habitat categories: 1) *Polylepis* forest specialists; 2) páramo specialists, occurring in páramo grassland, cushion páramo and shrubby páramo and prefer more open areas; and 3) generalists, species that use both of the aforementioned habitat categories.

Bird movements between patch and páramo matrix

We randomly installed a single point count ~80 m from the edge of each *Polylepis* patch in the páramo matrix, where we recorded all individual birds seen entering or leaving the patch in 50 minutes; we did not record birds that flew over the patch or did not perch on the surrounding matrix. We classified abundance as the average number of individuals which enter and leave a patch and richness as the total number of species moving between the patch and the matrix per locality. As the bird counts had many singletons, we used the Chao1 estimator to obtain a complete richness estimate (Chao 1984). However, for each habitat guild we only calculated the abundance; the richness of these guilds was not calculated due to the relatively low number of species registered per guild (Supplementary Table 4.3. see in Appendix).

Similarity between the patch and matrix

In the páramo matrix next to each *Polylepis* patch, we randomly established one 260 m strip transect ~200 m from the edge of the patch. Walking at a constant speed (~0.5 Km h^{-1}) we recorded all birds seen and heard within 30 m with all flyovers excluded (total counting area per locality= 7,800 m^2). Within each *Polylepis* patch, we randomly established four point counts separated by at least 150 m to avoid double counting and at least 80 m from the edge to minimize the influence from the páramo matrix. At each point count, we recorded all birds seen and heard in a radius of 25 m for 15 minutes with all flyovers excluded (total counting area per patch= 7,854 m^2). For the point counts and strip transect in each locality, we calculated bird abundance and a Sørensen quantitative similarity index. All diversity indices were calculated in EstimateS 9 (Colwell 2013).

Data analysis

We tested the influence of *Polylepis* patch area, nearest patch distance and páramo matrix complexity on estimated richness of movements using ANOVA. We used MANOVA to test for the influences of *Polylepis* patch area, nearest patch distance and páramo matrix complexity on the abundance of habitat guilds. Species similarity between the páramo matrix and *Polylepis* patch was tested with ANOVA (Zar 1984).All response variables were square root transformed to achieve homogeneity of variance and normality of residuals (Shapiro test: all *P* values > 0.13). The statistical analyses were performed in R 2.15.2 (R Development Core Team 2011) with alpha= 0.05. For PCA analysis we used the 'vegan' package (Oksanen 2011; Oksanen et al. 2011).

Results

In total, we recorded 318 individual movements of 25 bird species within the study area (Supplementary Table 4.3. see in Appendix). The number of species recorded across the 15 localities ranged from 2 to12 (6 ± 3; [mean, ± SD]), which was only slightly lower than the Chao1 estimated richness of 2 to 16 (6 ± 4; Supplementary Table 4.4. see in Appendix). Generalists accounted for 163 individual movements (51.25%), *Polylepis* specialists 87 movements (27.36%) and páramo specialists for 68 movements (21.30%; Supplementary Table 4.4. see in Appendix).

The estimated richness of movements was not influenced by either *Polylepis* patch area ($F_{1,11}$= 3.31, *P*= 0.09) nor by nearest patch distance ($F_{1,11}$= 3.18, *P*= 0.10), but it was positively related to PCI ($F_{1,11}$= 11.45, *P*<0.01; Fig. 2).

The similarity between *Polylepis* patch and páramo matrix ranged from 0.00 to 0.38 (0.20 ± 0.11; Supplementary Table 4.4. see in Appendix). Species similarity between the patch and matrix was neither influenced by patch area ($F_{1,11}$= 3.91, *P*= 0.07) nor nearest patch

distance ($F_{1,11}$= 0.95, P= 0.35); however, it increased significantly with increasing PCI ($F_{1,11}$= 10.40, P< 0.01; Fig. 2).

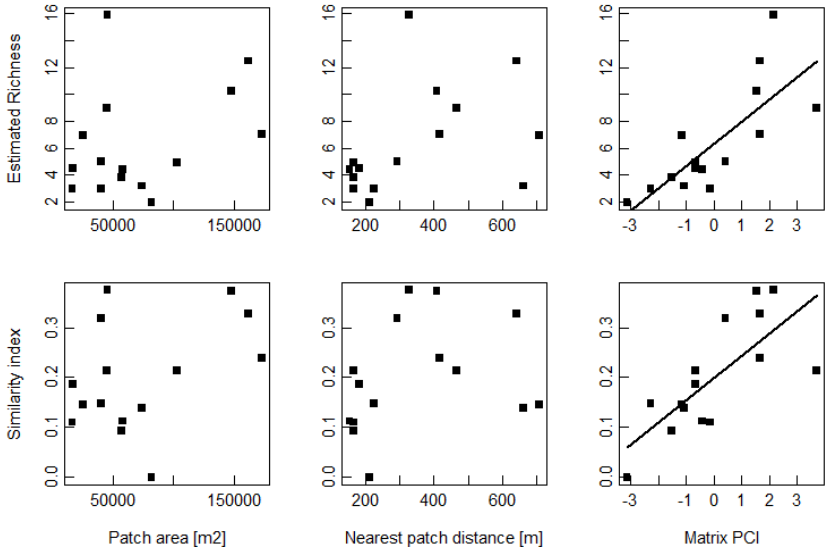

Figure 2. Influence of *Polylepis* patch area, nearest patch distance and páramo matrix complexity (PCI, increasing proportion of woody plants with higher vegetation profile) on estimated Chao1 richness based on species movements between the *Polylepis* patch and páramo matrix (upper panel) and on patch-matrix bird species similarity based on the Sørensen quantitative index (lower panel) across 15 localities in Cajas National Park, Ecuador. The plots with line tendency shown represent a significant relationship (P< 0.05).

The abundance of habitat guild movements was not influenced by patch area (Full model: $F_{2,11}$= 1.13, P= 0.39). However it was significantly positively influenced by both nearest patch distance (Full model: $F_{2,11}$= 5.18, P= 0.02) and by PCI (Full model: $F_{2,11}$= 8.69, P< 0.01). However, looking at guild-specific responses, for movements of *Polylepis* forest specialists we found a positive relationship with PCI ($F_{1,11}$= 8.33, P= 0.01) but not with patch area ($F_{1,11}$=, P= 0.38) or nearest patch distance ($F_{1,11}$= 0.96, P= 0.35). Movements of páramo specialists were neither influenced by patch area ($F_{1,11}$= 1.43, P= 0.26), nearest patch distance ($F_{1,11}$= 0.54, P= 0.49) nor PCI ($F_{1,11}$= 0.40, P= 0.48). Also movements of generalists were neither affected by patch area ($F_{1,11}$= 1.36, P= 0.27), nearest patch distance ($F_{1,11}$= 0.34, P= 0.57) nor PCI ($F_{1,11}$= 2.87, P= 0.12; Fig. 3).

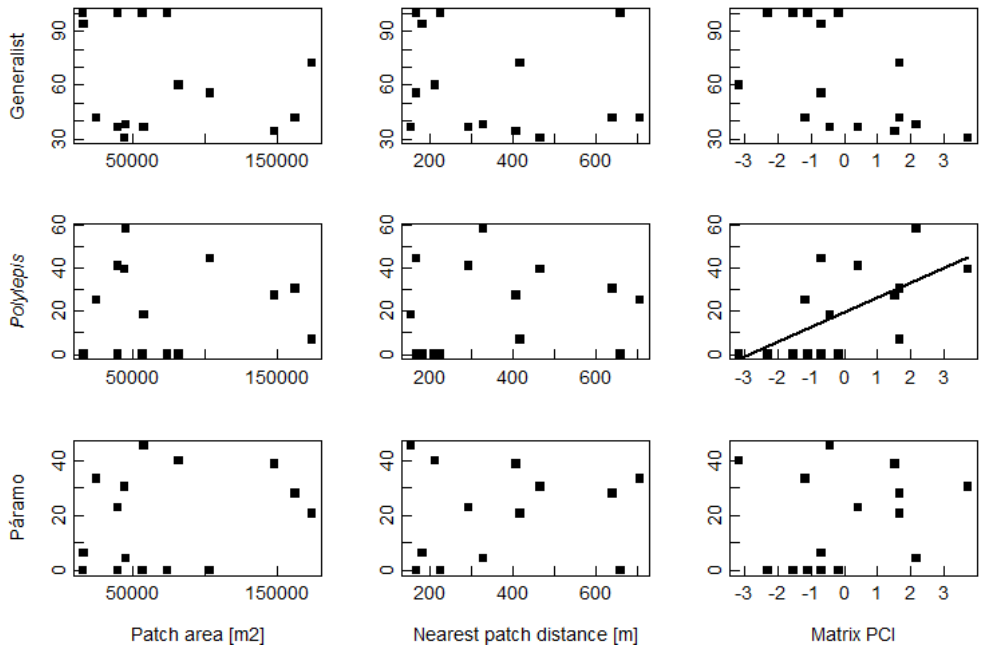

Figure 3 Influence of *Polylepis* patch area, distance to nearest patch and páramo matrix complexity (PCI, increasing proportion of woody plants with higher vegetation profile) on average abundance based on individual movements of each bird habitat guild across 15 localities in Cajas National Park, Ecuador. The plots with line tendency shown represent a significant relationship ($P < 0.05$).

Discussion

Our findings showed that a heterogeneous matrix, associated with an high proportion of both woody native páramo and cosmopolitan plants, increased the number of bird species and of *Polylepis* specialist individuals moving between *Polylepis* patches and the páramo matrix. This result was also reflected in a greater bird community similarity between the *Polylepis* patch and the matrix if the matrix is heterogeneous.

Many studies have shown that patch area positively influences species richness of birds (e.g. Robinson and Sherry 2012; Fahrig 2013) and these relationships have also been found in the study area (Tinoco et al. 2013). Our results do not follow this pattern. Other studies, however, support our result that *Polylepis* patch area does not influence species richness (e.g. Lloyd 2008a; Lloyd 2008b; Lloyd and Marsden 2008) and that the páramo matrix quality exerts a greater influence (Lloyd 2008b; Lloyd and Marsden

2011). This was also confirmed by Tinoco et al. (2013), who highlighted, besides the area effect, the positive relationship between abundance of *Gynoxys* plants in *Polylepis* patches and species richness. *Gynoxis* is associated with increasing páramo heterogeneity in our study we suspected this is not a uniquely related to single genus such as *Gynoxis* but to the matrix heterogeneity in general.

A more heterogeneous matrix has been shown to influence both animal diversity of forest fragments and landscape connectivity in other ecosystems as well (Tews et al. 2004; Robinson and Sherry 2012; Fahrig 2013; Neuschulz et al. 2013). Here, species can not only use the complex vegetation structures as corridors and stepping stones with reduced probabilities of predation (Baum et al. 2004), but for several birds, this complex matrix also provides sites for nesting and feeding resources (Fahrig 2013; Neuschulz et al. 2013; Vergara et al. 2013). This further enhances the connectivity between patches and reduces the negative effect of landscape fragmentation (Fahrig 2013; Baum et al. 2004).

Páramo matrix complexity also promotes bird similarity between the *Polylepis* patch and matrix. We believe that the increasing similarity of bird species is possibly a consequence of high movement activity between *Polylepis* patches due to the complex páramo matrix. A complex matrix attracts individual movements even of forest-specialist birds in fragmented landscapes (Baum et al. 2004; Neuschulz et al. 2013, Vergara et al. 2013). In fact, many studies have shown that habitat-specialist birds are strongly associated with the woody native plants of páramo ecosystems (Fjeldså and Krabbe 1990; Aguilar and Iñiguez 2011; Tinoco et al. 2013; Astudillo et al. 2014) and that their diversity is highly dependent on the increasing proportion of woody native plants throughout the páramo landscape (Astudillo et al. 2014).This complex matrix not only provides resources for forest birds directly, but also drives higher patch-matrix similarity of other animals, such as insects, whose similarity has been correlated to patch-matrix

similarity of birds (Su et al. 2004). In the páramo ecosystem, the woody native plants present inflorescences which attract arthropods, which in turn attract specialized birds (Aguilar and Iñiguez 2011; Astudillo et al. 2014). Similar patterns are reported in other fragmented forest landscapes (e.g. Baum et al. 2004; Robinson and Sherry 2012; Vergara et al. 2013). Such increasing similarity between patch and matrix may represent an important indicator other than species richness for conservation planning (Su et al. 2004; Latta et al. 2011).

Habitat quality of the patch itself has also been reported as an important factor for habitat-specialist birds, particularly for *Polylepis* specialists (Lloyd 2008a; Lloyd and Marsden 2011; Tinoco et al. 2013). However, isolated patches, even large and well-developed ones, may lose species over time (Robinson and Sherry 2012) and without sufficient connectivity they will not be replaced. In *Polylepis* forest a few studies have reported the role of small *Polylepis* patches as stepping stone for forest-specialist birds (e.g. Lloyd and Marsden 2011). However, within the study area a lack of information about movements of birds inhabiting *Polylepis* patches across the páramo matrix has been reported (Tinoco et al. 2013). Within this framework, it is important to establish a positive relationship between the numbers of individual-movements of *Polylepis* specialist birds and a complex habitat in páramo matrix. Our results suggest the importance of páramo matrix complexity for the whole bird community and particularly for *Polylepis* specialist movements.

Conservation remarks

The study provides clear evidence that in addition to area or distance to the next *Polylepis* patch, the structure and composition of páramo matrix is a highly important aspect of landscape connectivity. This is an important additional aspect as current conservation efforts on one of the most endangered habitats in the Andes (Renison et al. 2005; Benham et al. 2011) tend to orient towards *Polylepis* woodlands within the study are (Bucheli 2007). These results suggest that rather than focusing conservation efforts exclusively on the *Polylepis* patches themselves, stressors of páramo grassland should be seriously considered. For instance, the negative influence of grazing on bird abundance in the study area has been demonstrated for páramo birds with lower abundance in grazed areas, which are associated with a lower vegetation profile and less native woody plants (Samaniego et al. 2013). Besides, more recent human activities such as road construction, tourism and the introduction of non-native plants have strongly modified páramo grassland (Hofstede et al. 2002; CODESAN 2011; Astudillo et al. 2014). Removing this pressure, along with suppressing fire, is associated with increased shrub growth in páramo (Matson and Bart 2013) and such measures would benefit landscape connectivity for birds by increasing the heterogeneity of the páramo matrix. However, large-scale application of such management should be approached with caution as long-term effects of shrub encroachment on páramo plant communities is little investigated or understood (Matson and Bart 2014). The heterogeneity of páramo surrounding *Polylepis* patches, in particular greater native woody plant cover, could play a crucial role in maintaining biodiversity patterns at the landscape level.

5 Synthesis

My results demonstrated the importance of natural spatial heterogeneity on Andean high-altitude bird communities. This importance lays not only on the spatial configuration of *Polylepis* fragments, but also on that of the surrounding páramo. The major stressor, road infrastructure, passing through the páramo grassland is changing this natural habitat configuration at the roadsides influencing the composition of the bird community and decreasing the numbers of habitat-specialist birds. Furthermore, for *Polylepis* forest specialists the patch-centrality, have a positive relationship with the quality of fragments, altitude and regular shapes of forest. This in general, equates to a little modified landscape rather than to large *Polylepis* patches in particular; well-developed small and medium patches show the same trend. Furthermore, the surrounding páramo matrix also plays an important role in defining *Polylepis* patch connectivity of the landscape. Here, greater habitat complexity, led by an increasing proportion of woody native plants, is positively related to the number of *Polylepis* forest specialist individuals which moved between patch and matrix. The heterogeneity of the páramo matrix is also a very good predictor for shared species between patch and matrix.

The impact of roads on the avifauna of páramo grasslands in Cajas National Park, Ecuador

Along 15 km of the Cuenca-Molleturo-Naranjal road which passes through páramo grassland, I tested the effect of road proximity and habitat modification on species richness, abundance of four bird habitat groups (i.e. páramo specialists, shrubby páramo specialists, *Polylepis* specialists and generalists) and bird community composition. I did not find any influence of road proximity on species richness, although a change in the abundance of shrubby páramo specialists was demonstrated with significantly higher abundance far from the road (~ 250 m) than near the road (~ 25 m). Moreover, I found a tendency to separate the bird community recorded near and far from the road. These

changes in diversity patterns can be related to habitat modification due to an increasing proportion of non-native plants in the páramo grassland at the roadside.

These findings are the first to investigate road effects in the Andean region of Ecuador. More importantly, they suggest that the road facilitates the spread of non-native *Polylepis racemosa,* which is attracting a few páramo specialist birds but reducing the abundance of shrubby páramo specialists. The introduction of non-native plants may alter the natural habitat configuration of páramo grassland at the roadsides with consequent shifts in bird community composition, such as generalist species tending to be found near the road. Thus, I emphasize the importance to monitor avifauna at a community level to identify bird habitat guilds that appear to be more sensitive to road infrastructure and can also then be used as a good indicator for habitat modification associated to stressors in a páramo landscape.

Identifying the relative importance of forest structures for bird guilds: a landscape-wide network approach

Here I evaluated the connectivity among 15 *Polylepis* fragments via a network approach. Here, centrality indices were used to identify bird habitat guilds which are important connectors in the *Polylepis*-bird network. I used bird surveys within each patch to obtain the abundance of bird species as a value for patch-bird interaction. To interpret the connection between patches, the bipartite patch-bird network was converted to a unipartite representation, thus forest patches are connected to one another via shared species based on bird abundance. Furthermore, I used four different centrality measures to generate a composite centrality index (patch centrality) for forest patches, which was integrated for each respective bird habitat guild (i.e. *Polylepis* forest specialists, páramo specialists, and generalists). I explored the variation in the patch centrality for each bird

habitat guild with respect to patch altitude, patch-area, patch-shape, patch-habitat vegetation heterogeneity.

I found a positive relationship between the patch centrality for *Polylepis* specialists and patch altitude while the relationship between patch area and patch shape was negative. However, these two last predictors increase patch centrality for generalist birds. Habitat changes of patches - fragments with increasing influence from the native woody plants from surrounding matrix - reduced the patch centrality for *Polylepis* specialists and generalists. While fragments with increasing influences from both páramo restricted and widely distributed plants only decreased the composite centrality index for *Polylepis* specialists. All these findings show that the patch centrality for habitat specialists is highly dependent on both the quality of patches and the quality of the shrubby-grassland matrix. Consequently, conservation measures for these habitat-specialist birds should, in addition to preserving large patches of *Polylepis*, start to preserve smaller, high quality patches which may be used by forest specialists either temporarily or permanently in this fragmented landscape

Matrix heterogeneity enhances bird movement in a fragmented High-Andes landscape

Among the same 15 *Polylepis* patches, I explored how habitat heterogeneity of surrounding páramo, *Polylepis* patch area and also the distance to the nearest patch in the landscape influence the richness of bird movements (i.e. species entering and leaving the patch), abundance of bird movements (i.e. individuals entering and leaving the patch) and also the community similarity between patch and matrix. I postulated that the movements of *Polylepis* forest specialists are positively related to increasing proportion of woody

native plants in the páramo matrix, bigger patch areas and also closer neighborhood distance.

My results highlight the importance of habitat complexity in the páramo grassland matrix, where the increasing proportion of woody native plants in surrounding páramo increased species richness of bird movements, community similarity between patch and matrix as well as the abundance of *Polylepis* forest specialist movements. Patch area and distance to the nearest patch, however, did not influence movements. Thus, the heterogeneity in páramo grasslands provides a good indicator for conservation efforts in the high-altitude landscape. Indeed, I demonstrated that besides the *Polylepis* forest characteristic, the heterogeneity of surrounding páramo has a key role in enhancing the connectivity of the fragmented landscape. More importantly, while this connectivity is vital for the whole Andean bird community, it is especially important for habitat-specialist birds such as those of the *Polylepis* forest.

Conclusions

Bird communities in the high Andes are strongly influenced by habitat modification. Mainly due to the introduction of non-native *Polylepis racemosa*, the road infrastructure is a major stressor in the landscape. This introduction may alter the natural availability of páramo grassland affecting the diversity patterns of Andean birds and reducing the abundance of habitat-specialized birds. Within this framework these specialized species are particularly vulnerable to this stressor with consequent negative effects on their own survival. The findings of this study also point to the value of natural habitat heterogeneity within the páramo landscape. I found that the quality of *Polylepis* fragments with little influence from modified surrounding páramo and higher altitude promote greater connectivity for *Polylepis* forest specialists; while bigger patch areas with greater

influence from modified surrounding páramo are important for generalist species. Hence, these findings support the importance of high quality *Polylepis* woodlands whatever their size. I also demonstrated positive effects on movements between patch and matrix for the whole Andean bird community, but principally for *Polylepis* specialists, with increasing habitat complexity of the páramo matrix with evident profits for landscape connectivity.

Clearly, the páramo ecosystem is under threat, not only by road infrastructure itself, but also by many associated activities derived from road constructions, as highlighted in this study by the introduction of non-native plants. These activities, seemingly innocuous, are modifying the natural configuration of páramo, and unfortunately the managers of this natural area have the misplaced perception that the páramo grassland is an area where certain human practices can be tolerated. My results, however, confirm the importance of heterogeneous páramo grassland to enhance the connectivity within the landscape. Consequently, the loss of specialized birds in disturbed areas and also the positive effect of quality of *Polylepis* patches and their páramo matrix are crucial to a better understanding of the dynamics in the high-altitude Andes. Conservation efforts should not be concentrated solely on *Polylepis* forest; it is important to widen the focus to the landscape scale as other woody native habitats could play a vital role. Several protected areas in Ecuador include large areas of páramo ecosystems and all of them are highly threatened; hence, to promote effective nature conservation it is imperative to develop conservations plans that take into account natural habitat heterogeneity in the Andean region.

6 Future research perspectives

6 – Future research perspectives

This study definitely left several questions open that may concern conservation efforts in the Andean region of Ecuador. For instance, recent new habitat classifications of páramo ecosystems in the study area have defined five new plant associations separated by habitat structure and composition (Minga et al. 2013). These communities, similar to those for birds reported in this study, show specific associations at higher altitudes (> 3,900 m); two of these five habitat classifications are woody habitats, which were not well covered in this thesis. Particularly, a native woody formation dominated by *Loricaria illinisae* (Asteraceae) is clearly different from other woody native areas in the páramo landscape and shows a higher vegetation profile (~ 2 m) and a closer canopy cover (Minga et al. 2013). This newly defined habitat configuration may also enhance connectivity across the páramo landscape and it is imperative to understand bird diversity patterns and movements throughout the entire heterogeneous landscape and not only páramo associated to *Polylepis* forest. Besides, very little investigation into how forest-specialized birds use the páramo matrix has been done. One example comes from Aguilar and Iñiguez (2011) who reported that a single *Polylepis* specialist is willing to extend its home range into surrounding matrices. However, there is still a lack of information about which specific behavior (i.e. feeding, nesting, avoiding predation) occurs within these habitat-type matrices. Furthermore, to improve the understanding of the dynamics within the páramo ecosystem it would be important to explore in detail the pathways of movements, and define resistance or permeability of the páramo matrix heterogeneity.

Likewise, these perspectives could be also replicated in buffer areas to develop a stronger understanding of landscape dynamics throughout the Andean region. For example, the eastern high-altitude Andes are dominated by several native woody associations characterized by more complex habitat structures and different vegetation compositions where no *Polylepis* woodlands are found (Neill 1999; DIFORPA 2001).

This region is also influenced by roads but is also threatened by persistent agricultural practices and mining activities (MAE 2012). To understand effects of these stressors on bird community would not only be very interesting but important as diversity patterns between the east and west of Andes range are different (Fjeldså and Krabbe 1990; Ridgely and Greenfield 2001) and the results of this present study cannot be extrapolated.

Finally, there is a lack of information about trophic interactions occurring within páramo ecosystems. For instance, during the field work I observed high bird activity on specific plants; between November and December 2013, I recorded frugivorous species from lower forests feeding on fruits of *Miconia* plants and in March – April 2014, I observed several nectarivores feeding on flowers of *Hesperomeles*, *Churquiraga* and *Diplostephium*. It would be interesting to evaluate the mutualistic bird-plant interactions in *Polylepis* forest and páramo grassland and to evaluate if these interactions change across disturbance gradients (i.e. fires, grazing, introduction of non-native plants, touristic areas, buffer protected area). More importantly, it would be interesting to assess whether these interactions respond to land-use scenarios throughout the region, and if habitat-specialist birds are replaced in their niche by generalist from lower parts.

7 Deutsche Zusammenfassung

Landnutzungsänderungen wie Agrarexpansion und Urbanisierung führen zur Fragmentierung von Landschaften innerhalb der tropischen Anden. Diese Region gehört zu den Biodiversitätshotspots der Erde mit hohem Endemismus und hat folglich eine hohe Priorität bei Naturschutzmaßnahmen. Ecuador ist Teil der tropischen Anden und im Hochgebirge Ecuadors ist Habitatverlust bereits weit verbreitet und beständig.

Eine repräsentative Fläche für die Avifauna der Anden ist der Cajas Nationalpark. Dieser Park liegt in den südlichen Anden von Ecuador und ist die einzige geschützte Fläche in den südwestlichen Anden. Der Park besteht zu 90% aus Páramo-Grassland, welches mehr als 1000 Polylepis-Wald-Patches umschließt. Trotz seiner Bedeutung für den Vogelschutz und seines Schutzstatus' leidet der Cajas Nationalpark unter mehreren Stressoren, welche die natürlichen Habitatcharateristika sowohl des Páramos als auch der Polylepis-Patches verändern.

Daher haben wir untersucht, welchen Einfluss Straßen (als ein Hauptstressor), Habitatstruktur und Vegetationszusammensetzung sowohl der umgebenden Páramo-Matrix als auch der Polylepis-Patches auf die Vogelgemeinschaften haben.

Unsere Ergebnisse zeigen, dass Habitatspezialisten wie beispielsweise Strauch-Páramo-Vogelarten eine verringerte Abundanz in der Nähe der Straße aufwiesen, was auf die Habitatmodifizierung durch exotische Pflanzenarten zurückzuführen ist. Diese Habitatveränderungen in der Nähe der Straße führen zu deutlichen Änderungen in der Zusammensetzung der Vogelgemeinschaften hin zu wenigen Páramo-Spezialisten und

vielen Habitatgeneralisten. Darüber hinaus bestätigen unsere Ergebnisse die Bedeutung von natürlicher Habitatheterogenität des Páramos sowie von kleinen und mittelgroßen Polylepis-Patches für die Vogelgemeinschaften. Beispielsweise konnten wir einen positive Zusammenhang zwischen den Bewegungen von Polylepis-Spezialisten zwischen Patch und Matrix mit zunehmendem Anteil von holzigen Pflanzen in der Páramo-Matrix zeigen. Außerdem nahm für die Polylepis-Spezialisten der Zentralitätsindex der Polylepis-Patches auf höheren Höhenlagen zu.

Der Verlust von spezialisierten Vogelarten in gestörten Flächen und der positive Effekt von Polylepis-Patch-Qualität sowie Páramo-Heterogenität sind zentral für das Verständnis der Dynamiken in den Hochgebirgsbereichen der Anden. Zum Schutz der Vogelgemeinschaften ist daher ein Landschaftsansatz essentiell, der nicht nur große Polylepis-Patches schützt, sondern auch die Konnektivität berücksichtigt. Darüberhinaus können menschliche Aktivitäten in der Páramo-Landschaft zum Verlust der natürlichen Habitatheterogenität mit negativen Konsequenzen für Biodiversitätsmuster führen.

Mehrere Schutzgebiete in Ecuador beinhalten bereits große Flächen des Páramo-Ökosystems und alle sind stark bedroht. Um effektiven Naturschutz zu betreiben, ist es daher notwendig, Schutzkonzepte zu entwickeln, die diese natürliche Habitatheterogenität berücksichtigen – sowohl in Ecuador als auch in der gesamten Anden-Region.

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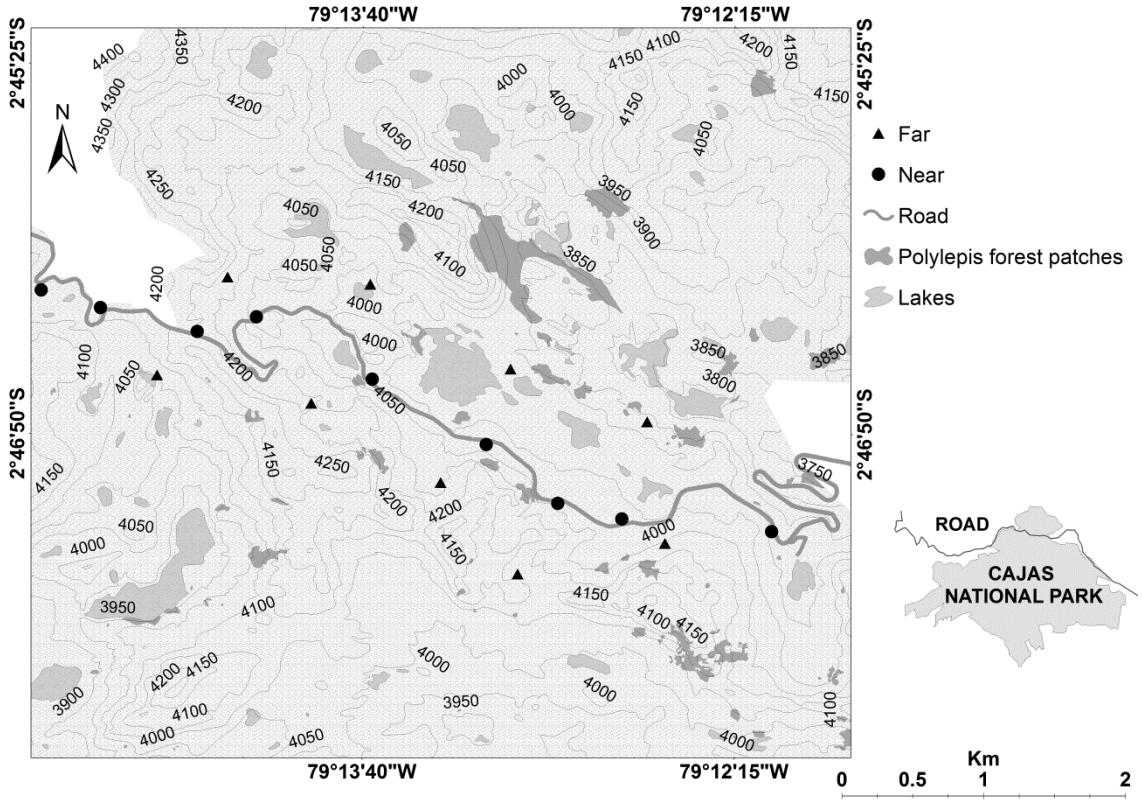
Appendix Chapter 2

The impact of roads on the avifauna of páramo grassland in Cajas National Park, Ecuador



Supplementary Figure 2.1. Study area and location of 18 strip transects within Cajas National Park, Ecuador. The filled triangles are the nine transects (1 km length) located far form road and the filled circles are the nine transects near the roadsides.

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Supplementary Table 2.1. Habitat characteristics across 18 transects (nine near, nine far) in Cajas National Park, Ecuador. Columns 3-8 were used to calculate principal components of vegetation structure.

		Habitat type (%)					
Distance	Transects	Woody Native shrubs	Non-native plants	Páramo grassland	Cushion páramo	Water	Rocky substrates
Near	T1	2.1	14.8	26.7	30.5	1.7	24.2
	T2	12.6	13.9	33.3	18.4	-	21.8
	T3	15.8	7.6	21.4	20.6	2.5	32.1
	T4	18	9.6	34.2	26.6	2.4	9.2
	T5	12.5	5.2	39.4	27.5	7.5	7.9
	T6	18.5	10	37.5	17	2.3	14.7
	T7	18.2	5.4	30.9	28.8	2	14.7
	T8	7.1	13.7	42.8	10.4	1.2	24.8
	T9	7.5	14.4	30.2	21.3	3	23.6
Far	T1	5.4	1.3	47.3	19.5	7.3	19.2
	T2	6.5	3.8	49.3	18.4	10	12
	T3	9.2	-	41.5	11	11.2	27.1
	T4	23.3	0.2	32.2	19.5	4.7	20.1
	T5	16.4	-	49.3	14.2	2.2	17.9
	T6	10.2	4.6	53.5	23.1	3	5.6
	T7	18.9	4.8	53.6	9.8	-	12.9
	T8	13.5	6.1	56	21.2	0.7	2.5
	T9	13.1	-	46	12.5	4.5	23.9

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Supplementary Table 3.1. Habitat group classification, species list and their average abundance near and far from road in Cajas National Park, Ecuador. Scientific and English names follow the South American committee (Remsen et al. 2013).

Habitat groups and species	English Name	Near		Far	
		Mean	±SD	Mean	±SD
Shrubby páramo					
Chalcostigma stanleyi	Blue-mantled Thornbill	11	3.61	8.33	0.58
Aglaeactis cupripennis	Shining Sunbeam	0.33	0.58	1.33	0.58
Asthenes flammulata	Many-striped Canastero	13.33	2.52	26.33	6.03
Oreotrochilus chimborazo	Ecuadorian Hillstar	3.67	0.58	12.67	3.21
Páramo					
Gallinago jamesoni	Andean Snipe	0.33	0.58	2.33	3.21
Cinclodes fuscus	Buff-winged Cinclodes	52.33	14.43	23.33	2.08
Cinclodes excelsior	Stout-billed Cinclodes	1.67	2.08	1	1
Muscisaxicola alpinus	Plain-capped Ground-Tyrant	3.33	1.53	1.33	0.58
Agriornis montanus	Black-billed Shrike-Tyrant	-	-	2.33	2.31
Cistothorus platensis	Sedge Wren	7.67	2.89	11	2.65
Phrygilus unicolor	Plumbeous Sierra-Finch	42.33	11.68	21	5.57
Catamenia inornata	Plain-colored Seedeater	2.67	2.52	3.33	2.89
Catamenia homochroa	Paramo Seedeater	0.33	0.58	0.33	0.58
Polylepis forest					
Mecocerculus leucophrys	White-throated Tyrannulet	1.33	1.15	0.33	0.58
Dubusia taeniata	Buff-breasted Mountain-Tanager	0.67	1.15	0.67	1.15
Oreomanes fraseri	Giant Conebill	1.33	1.15	0.67	0.58
Xenodacnis parina	Tit-like Dacnis	11.33	4.73	8	4.58

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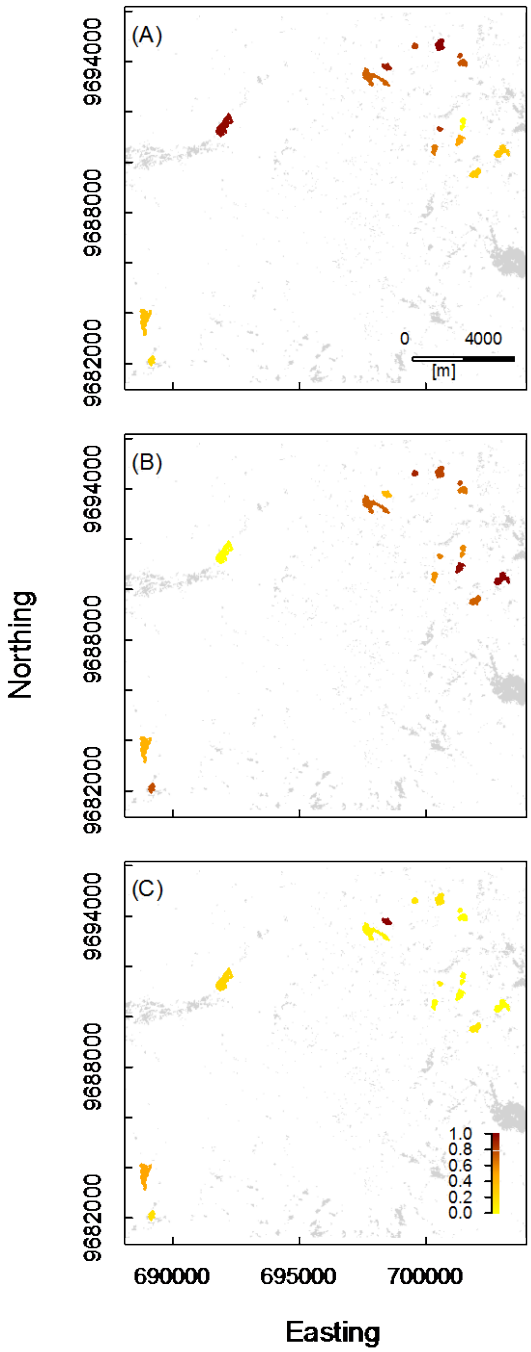
Habitat groups and species	English Name	Near		Far	
		Mean	±SD	Mean	±SD
Atlapetes latinuchus	Yellow-breasted Brush-Finch	1	1.73	-	-
Generalist					
Metallura baroni	Violet-throated Metaltail	12.67	6.11	5.67	2.08
Grallaria quitensis	Tawny Antpitta	15	1	11.67	2.31
Leptasthenura andicola	Andean Tit-Spinetail	5	2	5.33	3.51
Anairetes parulus	Tufted Tit-Tyrant	3	0.58	2.33	1.15
Cnemarchus erythropygius	Red-rumped Bush-Tyrant	-	-	1	1
Ochthoeca fumicolor	Brown-backed Chat-Tyrant	6	4.58	5	1
Turdus fuscater	Great Thrush	1.67	1.15	4	1
Conirostrum cinereum	Cinereous Conebill	2	1.73	-	-
Diglossa humeralis	Black Flowerpiercer	4.67	3.79	3.67	3.06
Zonotrichia capensis	Rufous-collared Sparrow	2.33	2.08	-	-

Appendix Chapter 3

Identifying the relative importance of forest structures for bird guilds: a landscape-wide network approach



Supplementary Figure 3.1. Map of the study area in Cajas National Park, Ecuador and the centrality of the 15 *Polylepis* forest patches (highlighted in color) included in this study. Patch centrality is shown for each bird guild separately: (A) *Polylepis* forest specialists; (B) generalists; and (C) páramo specialists. Centrality values are scaled between 0 and 1, with higher values indicating higher centrality within a given patch-bird guild network. Grey areas: other forest patches (with forest cover at a given pixel ≥ 50 %), based on a global forest cover dataset (Hansen et al. 2013). White areas: páramo matrix.

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Supplementary Table 3.1. General and environmental information on the 15 selected *Polylepis* patches. Columns 3−9 were used to calculate principal components of characteristics of each *Polylepis* patch (Supplementary Table 3.2.). Area, shape and altitude as well as the first two principal components of a PCA on plant diversity, vegetation profile and composition (see Methods) were used to predict the centrality of forest patches in the landscape-wide forest patch-bird guild networks. Spatial information (easting and northing of *Polylepis* patches) was included in spatial autoregressive models (SARs).

Forest patch name	Short name	Plant diversity	Vegetation profile	Canopy cover (0–4)	Median DBH [cm]	Woody native páramo plants [%]	Cosmopolitan woody native plants [%]	Woody *Polylepis* forest plants [%]	Easting	Northing	Perimeter [m]	Area [m²]	Shape	Altitude [m]
Ataudcocha	AT	1.21	2.24	3	93	3	60	37	698422	9693829	1467	44659	1.96	3929
Avilahuayco 1	AV1	1.56	2.21	2	101	17	50	32	701282	9690858	2221	57795	2.61	3947
Avilahuayco 2	AV2	1.88	1.96	3	77	23	50	26	700498	9691349	908	16484	1.99	3868
Avilahuayco 3	AV3	1.44	2.13	3	126	33	49	18	701464	9691717	1659	40004	2.34	3549
Barrancos 1	BA1	1.42	2.08	2	121	29	55	16	702057	9689684	2127	73926	2.21	3828
Barrancos 2	BA2	1.37	2.18	3	71	14	58	28	703010	9690515	3129	103371	2.76	3703
Chuspipuñuna 1	CH1	1.99	2.20	3	109	14	49	37	701443	9693991	1577	56993	1.86	3690
Chuspipuñuna 2	CH2	1.97	2.10	3	44	3	55	42	701354	9694282	492	15982	1.11	3745
Chuspipuñuna 3	CH3	1.35	2.13	3	117	9	56	34	700603	9694921	2480	81880	2.45	3863
Cucheros	CU	1.26	2.15	3	73	15	62	24	700314	9690636	1948	39960	2.75	4002
Derrumbo Amarillo	DA	1.16	2.23	4	92	4	69	27	699527	9694637	968	25107	1.72	4029
Dublaycocha 1	DN	1.75	1.99	3	82	33	45	21	689285	9684050	6439	147872	4.72	3947
Dublaycocha 2	DS	1.63	2.02	2	197	29	50	18	689133	9682190	1941	45206	2.58	3921
Huagrahuma	HU	1.12	2.03	3	28	3	27	70	692218	9691789	9067	162103	6.35	3767
San Luis	SL	1.35	2.13	3	99	15	67	18	697837	9693155	5677	173634	3.84	3913

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Supplementary Table 3.2. Factor loadings of patch characteristics of the 15 *Polylepis* patches from principal component analysis. The proportional variance by each component is given in brackets.

	PCI (39.6 %)	**PCII (28.8 %)**
Plant diversity	0.270	−0.241
Vegetation profile	−0.286	0.471
Canopy cover	−0.398	0.160
Median DBH	0.445	0.270
Woody native páramo plants	0.552	−0.040
Cosmopolitan woody native plants	−0.036	0.652
Woody *Polylepis* forest plants	−0.429	−0.442

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Supplementary Table 3.3. Factor loadings of centrality measures of forest patches from principal component analyses for each of the three bird guilds. The proportional variance explained by each component is given in brackets**.**

	Polylepis specialists				Generalists				Páramo specialists			
	PCI (67.5 %)	PCII (22.3 %)	PCIII (8.9 %)	PCIV (1.4 %)	PCI (69.1 %)	PCII (24.0 %)	PCIII (6.4 %)	PCIV (0.1 %)	PCI (98.0 %)	PCII (2.0 %)	PCIII (0.0 %)	PCIV (0.0 %)
Degree	−0.322	−0.876	−0.312	0.177	−0.188	0.969	0.052	−0.149	−0.056	−0.998	−0.026	−0.001
Opsahl degree	−0.487	0.419	−0.753	−0.142	−0.542	−0.126	0.817	0.153	−0.998	0.056	−0.022	0.003
Weighted closeness centrality	−0.572	0.224	0.362	0.702	−0.579	−0.211	−0.279	−0.736	−0.004	0.000	0.060	−0.998
Eigenvector centrality	−0.576	−0.086	0.453	−0.675	−0.579	0.013	−0.502	0.642	−0.023	−0.025	0.998	0.061

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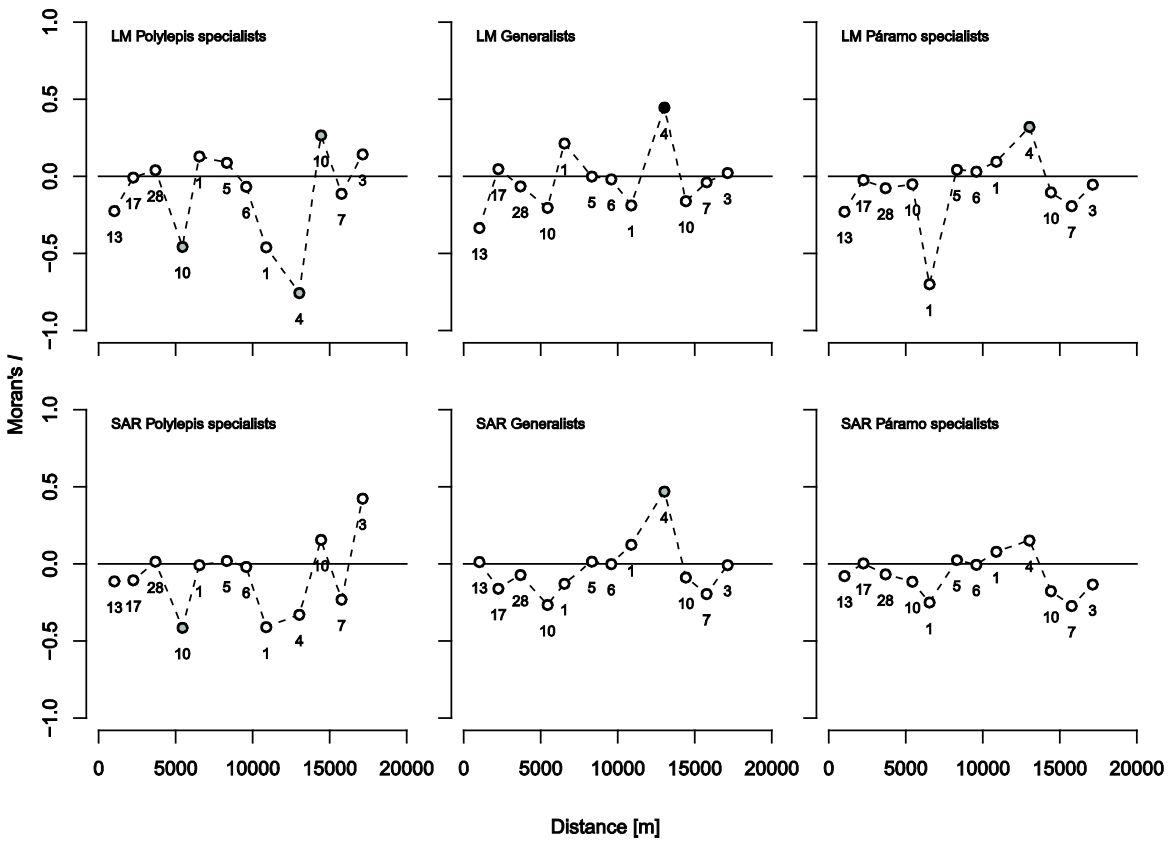

Supplementary Figure 3.2. Spatial autocorrelation (Moran's *I*) in the residuals of multiple linear regression models (LMs) and spatial autoregressive model (SARs) for each bird guild. Moran's *I* values were calculated in discrete distance classes of 1500 m; the number of pairs of study sites within each distance class is given below a given value. Circle colors indicate significance levels of values (black: $P < 0.01$, grey $P < 0.05$; white $P < 0.1$)

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Supplementary Table 3.4. Effects of patch characteristics of fragmented *Polylepis* forest on a) species richness and b) the Shannon diversity of Andean birds (*Polylepis* forest specialists, generalists and páramo specialists) in an Ecuadorian mosaic landscape. Note that effects of patch characteristics differ substantially from those were centrality measures of forest patches were investigated (Table 1, see in Results). Significant effects ($P < 0.05$) are highlighted in boldface type. Explanation of patch characteristics: area = patch area, shape = variation in shape irregularity independent of patch area, altitude = altitude of forest patch, PCI = influence of the surrounding páramo matrix on vegetative composition of forest patches, PCII = patch heterogeneity and influences from both *Polylepis* and páramo vegetation types.

		Polylepis specialists				Generalists				Páramo specialists			
		Estimate	SE	Z	P	Estimate	SE	Z	P	Estimate	SE	Z	P
a) Bird richness	Intercept	**7.328**	**0.139**	**52.602**	**< 0.001**	**5.406**	**0.063**	**85.637**	**< 0.001**	**0.945**	**0.096**	**9.859**	**< 0.001**
	Area	0.001	0.238	0.005	0.996	−0.032	0.105	−0.308	0.758	0.184	0.147	1.249	0.212
	Shape	0.003	0.303	0.009	0.993	0.058	0.133	0.440	0.660	−0.071	0.187	−0.379	0.705
	Altitude	−0.123	0.311	−0.395	0.693	0.064	0.133	0.477	0.634	0.232	0.180	1.289	0.198
	PCI	**−0.404**	**0.197**	**−2.050**	**0.040**	**0.213**	**0.087**	**2.443**	**0.015**	0.022	0.127	0.174	0.862
	PCII	−0.091	0.378	−0.240	0.810	−0.313	0.164	−1.910	0.056	−0.297	0.225	−1.323	0.186

		Polylepis specialist				Generalist				Páramo specialists			
		Estimate	SE	Z	P	Estimate	SE	Z	P	Estimate	SE	Z	P
b) Bird diversity	Intercept	**1.519**	**0.040**	**38.143**	**< 0.001**	**1.468**	**0.013**	**114.255**	**< 0.001**	**0.357**	**0.041**	**8.636**	**< 0.001**
	Area	−0.003	0.045	−0.062	0.951	−0.022	0.023	−0.959	0.337	**0.139**	**0.064**	**2.168**	**0.030**
	Shape	−0.024	0.060	−0.405	0.686	−0.002	0.029	−0.072	0.942	−0.024	0.082	−0.293	0.770
	Altitude	0.018	0.050	0.359	0.720	0.004	0.030	0.120	0.904	0.174	0.079	2.199	0.028
	PCI	0.025	0.043	0.585	0.559	**0.064**	**0.018**	**3.475**	**0.001**	**0.129**	**0.055**	**2.346**	**0.019**
	PCII	−0.002	0.064	−0.035	0.972	**−0.113**	**0.036**	**−3.117**	**0.002**	**−0.317**	**0.099**	**−3.213**	**0.001**

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Supplementary Table 3.5. Habitat group classification, species list and their total abundance across 15 *Polylepis* patches in Cajas National Park, Ecuador.

Habitat group and species	Locality code														
	AT	AV1	AV2	AV3	BA1	BA2	CH1	CH2	CH3	CU	DA	DU1	DU2	HU	SL
Generalist															
Bubo virginianus	-	2	-	-	-	-	-	-	-	-	1	2	3	1	-
Carduelis magellanica	7	1	-	1	7	-	3	2	15	17	17	8	1	11	4
Cnemarchus erythropygius	-	-	1	3	1	-	-	7	-	1	-	-	-	-	-
Grallaria quitensis	8	7	15	10	4	13	6	7	5	11	6	7	9	16	10
Metallura baroni	29	6	17	11	12	11	16	10	9	8	2	15	12	12	18
Ochthoeca fumicolor	5	6	7	9	11	4	2	7	4	-	9	15	6	9	1
Turdus fuscater	3	4	5	12	6	3	21	4	3	12	-	3	4	20	5
Polylepis forest															
Anisognathus igniventris	-	1	6	6	1	-	3	-	1	3	-	-	7	-	-
Atlapetes latinuchus	-	-	-	-	2	-	-	-	-	-	-	-	-	6	-
Boissonneaua matthewsii	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-
Cyanolyca turcosa	-	-	-	-	-	5	2	-	-	-	-	-	-	-	-
Diglossa humeralis	4	-	2	-	-	-	-	-	-	-	-	-	-	4	6
Dubusia taeniata	4	2	-	-	-	-	-	-	2	-	-	3	3	-	2
Elaenia albiceps	-	2	-	-	-	-	-	-	-	-	-	-	4	-	-
Margarornis squamiger	1	7	5	2	1	11	2	9	1	11	10	6	-	2	1
Mecocerculus leucophrys	30	21	26	14	12	13	42	33	32	30	30	29	23	39	26
Myioborus melanocephalus	-	-	15	-	-	3	9	19	5	-	2	-	2	3	1
Oreomanes fraseri	-	8	2	-	9	-	-	7	8	5	7	9	2	9	8

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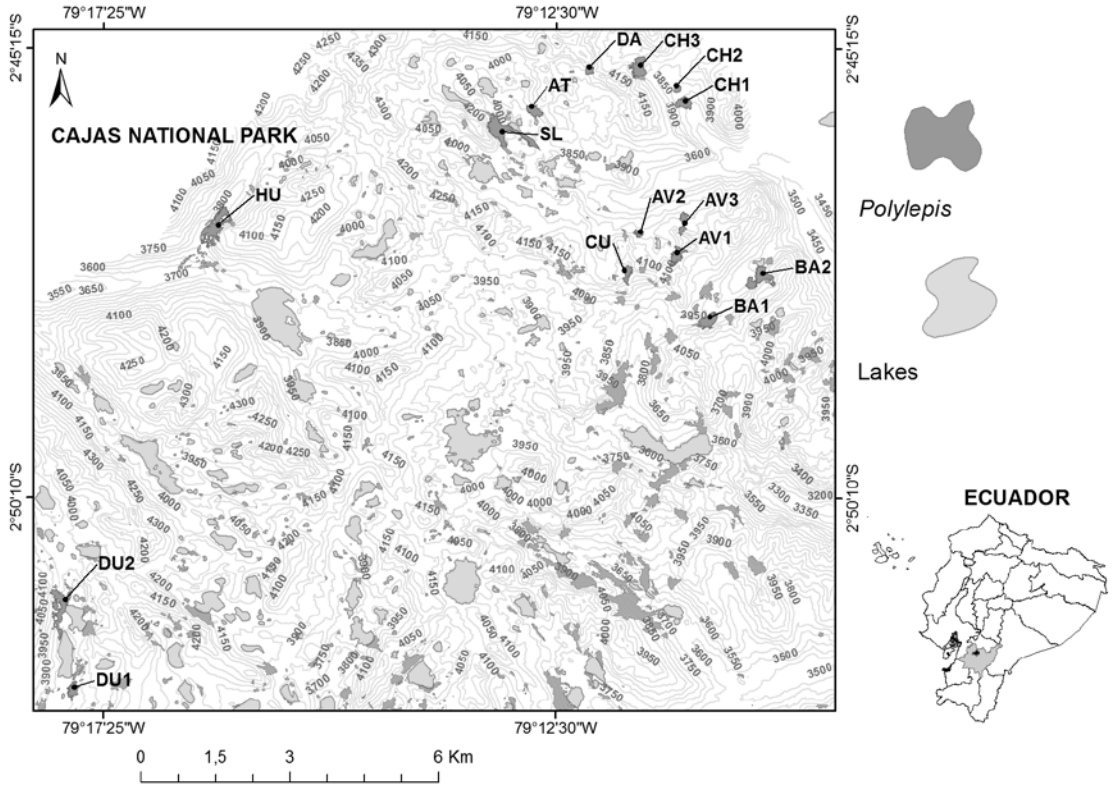
Habitat group and species	Locality code														
	AT	AV1	AV2	AV3	BA1	BA2	CH1	CH2	CH3	CU	DA	DU1	DU2	HU	SL
Pterophanes cyanopterus	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-
Schizoeaca griseomurina	2	-	4	1	2	4	-	3	5	2	5	3	5	2	-
Scytalopus latrans	3	2	8	7	7	14	1	1	5	-	6	-	-	4	6
Xenodacnis parina	39	6	-	1	6	-	-	-	24	8	4	-	-	1	21
Páramo															
Cistothorus platensis	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Cinclodes excelesior	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
Cinclodes fuscus	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Aglaeactis cupripennis	-	-	-	-	-	-	-	-	-	-	-	5	-	2	-
Asthenes flammulata	-	-	-	-	3	-	-	1	-	-	-	-	3	4	2
Chalcostigma herrani	-	-	-	-	-	-	-	-	1	-	-	-	3	-	-
Chalcostigma stanleyi	35	-	1	3	1	-	-	-	4	-	5	5	-	2	-
Leptasthenura andicola	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Oreotrochilus chimborazo	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-

Appendix Chapter 4

Matrix heterogeneity enhances bird movement in a fragmented High-Andes landscape



Supplementary Figure 4.1. Study area of 15 study localities in Cajas National Park, Ecuador. Each locality is a single patch of *Polylepis* woodland surrounded by páramo grassland**.**

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Supplementary Table 4.1. Páramo-habitat characteristics, *Polylepis* patch area and distance of nearest patch across 15 localities in Cajas National Park, Ecuador. Rows 2-9 were used to principal component analysis of matrix habitat structure.

Habitat variable	AT	AV1	AV2	AV3	BA1	BA2	CH1	CH2	CH3	CU	DA	DU1	DU2	HU	SL
Páramo Grassland (%)	18.8	72.5	75	97.3	87.5	65	88.3	58.8	93.3	65	81	58	52.3	37.5	45
Rocky substrates (%)	33.8	-	-	-	3.3	-	-	13.3	-	-	6.3	2	5.8	7.5	7.5
Water bodies (%)	-	0.8	-	1	-	2.5	-	1.3	3.3	-	-	-	-	1.5	0.5
Native woody páramo shrubs (%)	36.3	25.8	22	1.3	6.8	28.8	10.5	18.0	1.6	20.3	12.8	16	19.3	16	35.8
Cosmopolitan woody plants (%)	11.3	-	3	0.5	2.5	3.8	-	6.3	1.6	11.8	-	14	15.8	27.3	6.3
Polylepis forest plants (%)	-	1	-	-	-	-	1.3	2.5	-	3	-	10	7	10.3	5
Shannon plant diversity	0.5	1.1	1.5	1.4	1.7	1.2	1.3	1.1	1.5	1.6	0.8	0.4	1.9	1.4	1.8
Shannon vertical complexity	1.3	0.8	0.7	0.6	0.9	0.8	0.7	0.5	0.5	1	0.5	0.9	1.5	0.6	1.1
Polylepis patch area (ha)	4.5	5.8	1.6	4	7.4	10.3	5.7	1.6	8.2	4	2.5	14.8	4.5	16.2	17.4
Distance of nearest patch (m)	466.4	154.6	181.7	225.9	659.8	167.5	167.5	167.5	212.1	293.3	707.4	408.7	328.8	640.6	417.7

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Supplementary Table 4.2. Eigenvectors of the principal component analysis of the habitat variables of surrounding páramo in 15 localities in Cajas National Park, Ecuador. The variance accounted for 35.27% and PCII 20.57%

Habitat variable	PCI	PCII
Cushion páramo (%)	-0.33	-0.49
Páramo grassland (%)	-0.29	0.60
Rocky substrates (%)	0.38	-0.24
Water bodies (%)	-0.24	-0.49
Native woody páramo shrubs (%)	0.41	-0.03
Cosmopolitan woody plants (%)	0.40	-0.13
Polylepis forest plants (%)	0.32	-0.02
Shannon plant diversity	-0.11	0.20
Shannon vertical complexity	0.41	0.20

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Supplementary Table 4.3. Species list, habitat guild classification and average abundance based on observed movements across 15 localities in Cajas National Park, Ecuador.

Species	Name	Habitat guild	Mean	±SD
Bubo virginianus	Great Horned Owl	Generalist	0.83	0.75
Oreotrochilus chimborazo	Ecuadorian Hillstar	Páramo	1.67	0.82
Chalcostigma stanleyi	Blue-mantled Thornbill	Páramo	2.67	1.21
Chalcostigma herrani	Rainbow-bearded Thornbill	Páramo	0.67	0.82
Metallura baroni	Violet-throated Metaltail	Generalist	3.5	2.88
Aglaeactis cupripennis	Shining Sunbeam	Páramo	1.83	1.47
Grallaria quitensis	Tawny Antpitta	Generalist	0.83	0.75
Margarornis squamiger	Pearled Treerunner	*Polylepis* forest	0.33	0.82
Leptasthenura andicola	Andean Tit-Spinetail	Generalist	0.17	0.41
Asthenes griseomurina	Mouse-colored Thistletail	*Polylepis* forest	0.67	0.52
Mecocerculus leucophrys	White-throated Tyrannulet	*Polylepis* forest	2.33	1.97
Anairetes parulus	Tufted Tit-Tyrant	*Polylepis* forest	1	1.1
Agriornis montanus	Black-billed Shrike-Tyrant	Páramo	0.33	0.52
Cnemarchus erythropygius	Red-rumped Bush-Tyrant	Generalist	3.17	1.72
Ochthoeca fumicolor	Brown-backed Chat-Tyrant	Generalist	6.83	1.47
Turdus fuscater	Great Thrush	Generalist	7.33	3.33
Anisognathus igniventris	Scarlet-bellied Mountain-Tanager	*Polylepis* forest	0.33	0.52
Oreomanes fraseri	Giant Conebill	*Polylepis* forest	1	0.89

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Species	Name	Habitat guild	Mean	±SD
Xenodacnis parina	Tit-like Dacnis	*Polylepis* forest	0.67	0.82
Diglossa humeralis	Black Flowerpiercer	*Polylepis* forest	0.33	0.52
Phrygilus unicolor	Plumbeous Sierra-Finch	Páramo	1	1.26
Catamenia inornata	Plain-colored Seedeater	Páramo	0.33	0.82
Catamenia homochroa	Paramo Seedeater	Páramo	0.17	0.41
Myioborus melanocephalus	Spectacled Redstart	*Polylepis* forest	0.33	0.52
Sporagra magellanica	Hooded Siskin	Generalist	1.33	1.03

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Supplementary Table 4.4. Total richness based on species movements, Chao 1 species richness estimator, similarity between *Polylepis* patch and páramo matrix based on Sørensen quantitative index and average abundance of bird habitat guilds based on movements of each guild across 15 localities in Cajas National Park, Ecuador.

Locality code	Richness	Chao1 (± SD)	CI (95%)	Patch-Matrix Similarity	Habitat guild (± SD)		
					Generalist	*Polylepis* specialist	Páramo specialist
AT	8	8.97(±1.44)	7.98-9.96	0.21	1.83(±1.03)	2.5(±2.79)	1.67(±1.03)
AV1	4	4.45(±0.95)	3.52-5.38	0.11	0.67(±0.82)	0.33(±0.52)	0.83(±0.41)
AV2	4	4.47(±1.03)	3.46-5.48	0.19	2.5(±1.64)	-	0.167(±0.41)
AV3	3	3(±0.68)	2.23-3.77	0.15	1.67(±1.21)	-	-
BA1	3	3.2(±0.95)	2.13-4.27	0.14	0.83(±0.98)	-	-
BA2	4	4.89(±1.5)	3.42-6.36	0.21	1.5(±1.60)	0.83(±1.63)	-
CH1	3	3.86(±1.04)	2.68-5.64	0.09	1.17(±0.98)	-	-
CH2	3	3(±0.47)	2.47-3.53	0.11	3.33(±1.38)	-	-
CH3	2	2(±0.6)	1.17-2.83	0.00	0.17(±1.22)	-	0.33(±0.82)
CU	5	5(±0.86)	4.24-5.76	0.32	1.33(±0.82)	1.83(±2.74)	0.83(±0.75)
DA	6	6.96(±1.8)	5.52-8.4	0.15	1.67(±1.51)	1(±2.45)	1.33(±1.75)
DU1	9	10.24(±1.85)	9.09-11.39	0.37	2.5(±2.35)	0.67(±2.28)	2.83(±2.56)
DU2	12	15.91(±3.83)	13.97-17.85	0.38	2.83(±1.17)	3.67(±4.93)	0.33(±0.82)
HU	11	12.47(±3.08)	10.73-14.21	0.33	3(±1.26)	1.67(±2.04)	2(±2.9)
SL	7	7(±1.56)	5.85-8.15	0.24	3.5(±1.52)	0.33(±0.52)	1(±1.10)

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Supplementary Table 4.5. Habitat guild classification, species list and their total abundance across 15 localities in Cajas National Park, Ecuador. The classification is separated by birds which were recorded in *Polylepis* patches (patch counts) and páramo matrix (matrix transects). These values were used by calculated Sørensen quantitative index between patch-matrix (Supplementary Table 4.4.).

Habitat group and species	Locality code														
	AT	AV1	AV2	AV3	BA1	BA2	CH1	CH2	CH3	CU	DA	DU1	DU2	HU	SL
Patch counts															
Generalist															
Bubo virginianus	-	2	-	-	-	-	-	-	-	-	1	2	3	1	-
Carduelis magellanica	7	1	-	1	7	-	3	2	15	17	17	8	1	11	4
Cnemarchus erythropygius	-	-	1	3	1	-	-	7	-	1	-	-	-	-	-
Grallaria quitensis	8	7	15	10	4	13	6	7	5	11	6	7	9	16	10
Leptasthenura andicola	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Metallura baroni	29	6	17	11	12	11	16	10	9	8	2	15	12	12	18
Ochthoeca fumicolor	5	6	7	9	11	4	2	7	4	-	9	15	6	9	1
Turdus fuscater	3	4	5	12	6	3	21	4	3	12	-	3	4	20	5
Páramo															
Cinclodes excelesior	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-
Cinclodes fuscus	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Cistothorus platensis	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Aglaeactis cupripennis	-	-	-	-	-	-	-	-	-	-	-	5	-	2	-
Asthenes flammulata	-	-	-	-	3	-	-	1	-	-	-	-	3	4	2
Chalcostigma herrani	-	-	-	-	-	-	-	-	1	-	-	-	3	-	-
Chalcostigma stanleyi	35	-	1	3	1	-	-	-	4	-	5	5	-	2	-
Oreotrochilus chimborazo	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-

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Habitat group and species	Locality code														
	AT	AV1	AV2	AV3	BA1	BA2	CH1	CH2	CH3	CU	DA	DU1	DU2	HU	SL
Polylepis forest															
Anisognathus igniventris	-	1	6	6	1	-	3	-	1	3	-	-	7	-	-
Atlapetes latinuchus	-	-	-	-	2	-	-	-	-	-	-	-	-	6	-
Boissonneaua matthewsii	-	-	-	-	-	-	5	-	-	-	-	-	-	-	-
Cyanolyca turcosa	-	-	-	-	-	5	2	-	-	-	-	-	-	-	-
Diglossa humeralis	4	-	2	-	-	-	-	-	-	-	-	-	-	4	6
Dubusia taeniata	4	2	-	-	-	-	-	-	2	-	-	3	3	-	2
Elaenia albiceps	-	2	-	-	-	-	-	-	-	-	-	-	4	-	-
Margarornis squamiger	1	7	5	2	1	11	2	9	1	11	10	6	-	2	1
Mecocerculus leucophrys	30	21	26	14	12	13	42	33	32	30	30	29	23	39	26
Myioborus melanocephalus	-	-	15	-	-	3	9	19	5	-	2	-	2	3	1
Oreomanes fraseri	-	8	2	-	9	-	-	7	8	5	7	9	2	9	8
Pterophanes cyanopterus	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-
Schizoeaca griseomurina	2	-	4	1	2	4	-	3	5	2	5	3	5	2	-
Scytalopus latrans	3	2	8	7	7	14	1	1	5	-	6	-	-	4	6
Xenodacnis parina	39	6	-	1	6	-	-	-	24	8	4	-	-	1	21
Matrix transect															
Generalist															
Cnemarchus erythropygius	-	-	-	2	3	-	-	-	-	-	-	7	2	5	-
Grallaria quitensis	7	2	6	5	8	5	5	5	-	9	8	11	3	9	10
Leptasthenura andicola	-	2	1	2	-	4	4	6	4	2	4	4	3	5	3
Metallura baroni	7	3	5	1	-	6	2	2	-	4	3	3	2	5	4
Ochthoeca fumicolor	4	1	1	1	2	1	-	-	-	1	-	11	7	-	-
Turdus fuscater	2	-	1	1	-	-	-	-	-	-	-	3	9	15	2
Zonotrichia capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-

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Habitat group and species	Locality code														
	AT	AV1	AV2	AV3	BA1	BA2	CH1	CH2	CH3	CU	DA	DU1	DU2	HU	SL
Páramo	13	12	16	14	12	12	19	14	23	14	16	17	17	34	24
Agriornis montana	2	1	4	2	-	-	5	1	2	-	-	2	-	2	9
Catamenia homochroa	-	-	-	1	-	3	-	-	-	-	-	-	-	-	-
Cinclodes excelesior	-	-	-	-	-	3	-	-	7	-	2	-	-	2	-
Cinclodes fuscus	9	4	2	4	9	4	7	7	14	4	11	11	4	12	8
Cistothorus platensis	1	7	9	1	-	1	1	4	-	4	-	-	10	-	6
Muscisaxicola alpina	-	-	-	2	-	-	2	-	-	-	-	1	-	11	-
Phrygilus unicolor	1	-	1	4	3	1	4	2	-	6	3	3	3	7	1
Aglaeactis cupripennis	-	-	-	-	-	-	-	-	-	-	-	4	-	2	-
Asthenes flammulata	1	6	4	3	2	3	5	9	2	2	1	4	9	1	8
Chalcostigma herrani	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-
Chalcostigma stanleyi	-	3	-	-	-	-	-	-	-	8	-	3	2	1	2
Oreotrochilus chimborazo	-	1	-	-	2	-	1	-	-	3	-	3	-	4	-
Polylepis forest															
Anisognathus igniventris	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-
Atlapetes latinuchus	-	-	-	-	-	-	-	-	-	-	-	-	2	10	-
Margarornis squamiger	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-
Mecocerculus leucophrys	-	-	-	-	-	-	-	-	-	4	-	4	9	2	-
Oreomanes fraseri	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
Schizoeaca griseomurina	-	2	-	-	-	-	-	-	-	1	-	2	2	-	2
Scytalopus latrans	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
Xenodacnis parina	2	-	-	-	-	-	-	-	-	7	2	-	1	14	2

9 References

9 – References

Aguilar J and Iñiguez X (2011) Requerimientos de Hábitat del Azulito Altoandino (*Xenodacnis parina, Cabanis*, 1873) en la microcuenca del Río Matadero, Bach. thesis. Cuenca (Ecuador): Universidad del Azuay.

Armenteras D, Gast F and Villareal H (2003) Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. Biological Conservation. 113:245–256.

Astudillo PX, Samaniego GM, Machado PJ, Aguilar JM, Tinoco BA, Graham CH and Farwig N (2014) The impact of roads on the avifauna of páramo grasslands in Cajas National Park, Ecuador. Studies on Neotropical Fauna and Environment. in press: DOI: 10.1080/01650521.2014.960778

Baquero F, Sierra R, Ordóñez L, Tipán M, Espinosa L, Rivera M and Soria P (2004) La vegetación de los Andes del Ecuador. (Quito, Ecuador): EcoCiencia, CESLA, Corporación EcoPar, MAG SIGAGRO, CDC JatunSacha, División Geográfica-IGM.

Barnett TP, Adam C and Lettenmaier P (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. Nature. 438: 303–309.

Baum KA, Haynes JK, Dillemuth PF and Cronin TJ (2004) The matrix enhances the effectiveness of corridors and stepping stones. Ecology. 85: 2671–2676.

Beissinger SR and Osborne DR (1982) Effects of urbanization on avian community organization. Condor. 84: 75-83.

Benham PM, Beckman EJ, Dubay SG, Flores LM, Johnson AB, Lelevier MJ and Witt CC (2011) Satellite imagery reveals new critical habitat for endangered bird species in the high Andes of Peru. Endangered Species Research. 13: 145–157.

9 – References

Berens DG, Chama L, Albrecht J and Farwig N (2014) High conservation value of forest fragments for plant and frugivore communities in a fragmented forest landscape in South Africa. Biotropica. 46: 350-356.

BirdLife International. (2004) Threatened birds of the world. BirdLife International, Cambridge (UK).

Bryan K. and Leise T. (2006) The $25,000,000,000 eigenvector: the linear algebra behind Google. SIAM Review. 48: 569–581.

Bucheli GF. (2007) Parque Nacional Cajas una oportunidad para la vida y el desarrollo local sustentable. (Cuenca, Ecuador): Empresa Municipal de Telecomunicaciones, Agua Potable, Alcantarillado y Saneamiento Ambiental de Cuenca.

Cahill JR and Matthysen E (2007) Habitat use by two specialist birds in high-Andean *Polylepis* forests. Biological Conservation. 140: 62–69.

Camp M and Best LB (1993) Bird abundance and species richness in roadsides adjacent to Iowa rowcrop fields. Wildlife Society Bulletin. 21: 315-325.

Camp M and Best LB (1994) Nest density and nesting success of birds in roadside adjacent to rowcrop fields. American Midland Naturalist. 131: 347-358.

Carrión J. (2000) Breves consideraciones sobre la avifauna paramera del Ecuador. In: La biodiversidad de los Páramos. Serie Páramo 7. Quito: GTP & Abya Yala.

Celleri, R, Willems P, Buytaert W and Feyem J (2007) Space – time rainfall variability in the Paute Basin, Ecuadorian Andes. Hydrilogical Process. 21: 3316–3327.

Chao A (1984) Nonparametric estimation of the number of classes in a population. Scandinavian Journal of Statistics 11:265-270.

9 – References

Chapman FM (1926) The distribution of bird-life in Ecuador. Bulletin of the American Museum of Natural History. 55: 1-784.

Clergeau P, Savard JL, Mennechez G and Falardeau G (1998) Bird abundance and diversity along an urban-rural gradient: A comparative study between two cities on different continents. Condor, 100: 413-425.

CODESAN (2011) Los riesgos de la reforestación de los páramos con especies exóticas: El caso *Polylepis racemosa*. (Quito, Ecuador): Consorcio para el desarrollo de la ecoregión andina y su proyecto páramo andino. Propuestas Andinas Páramo.

Colwell RK (2006) EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. Persistent URL <purl.oclc.org/estimates> (accessed 19 November 2013).

Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. Persistent URL <purl.oclc.org/estimates> (accessed 03 August 2014).

Cursach AJ and Rau JR (2008) Influencia de las perturbaciones humanas sobre la diversidad del ensamble de aves costeras en el seno de Reloncaví, sur de Chile. Boletín Chileno de Ornitología. 14: 92-97.

Debinski DM and Holt RD (2000) A Survey and Overview of Habitat Fragmentation Experiments. Conservation Biology 14: 342–355.

Delgado O, López F, Aguilar M and Cordero M (2006) Componente geomorfología glaciar del Parque Nacional Cajas – Ecuador. Unpublished report. (Cuenca, Ecuador): Universidad del Azuay.

9 – References

Devenish C, Díaz-Fernández DF, Clay RP, Davidson I and Yépez-Zabala I (eds.) (2009) Important Bird Areas Americas – Priority sites for biodiversity conservation. (Quito, Ecuador): BirdLife International, BirdLife Conservation Series No. 16.

DIFORPA. (2001) Diversidad Forestal de la Cuenca del Río Paute. Unpublished report. (Cuenca, Ecuador): UDA – FUNDACYT.

Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G and Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography, 30: 609–628.

Encalada O (2009) Monitoreo y evaluación de la eficiencia del manejo del Parque Nacional Cajas. (Cuenca, Ecuador): Empresa Municipal de Telecomunicaciones, Agua Potable, Alcantarillado y Saneamiento Ambiental de Cuenca.

Etter A and van Wyngaarden W (2000) Patterns of Landscape Transformation in Colombia, with Emphasis in the Andean Region. A Journal of the Human Environment. 29:432–439.

Fahrig L (2013) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology and Systematic. 34: 487–515.

Fahrig L and Rytwinski T (2009) Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society. 14: 21-41.

Fischer J and Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography. 16: 265–280.

9 – References

Fjeldså J (1993) The avifauna of the *Polylepis* woodlands of the Andean highlands: the efficiency of basing conservation priorities on patterns of endemism. Bird Conservation International. 3: 37–55.

Fjeldså J (2002) Key areas for conserving the avifauna of *Poylepis* forest. Ecotropica 8: 125 – 131.

Fjeldså J and Krabbe N (1990) Birds of the high Andes. Svendlborg: University of Copenhagen and Apollo Books.

Flores E (2013) La ordenación de la red vial del cantón Cuenca. Master Thesis. (Cuenca, Ecuador): Universidad. de Cuenca.

Foley JA, Defries R, Asner GP, Barford C, Bonan G, Carpenter SR and Snyder PK (2005) Global consequences of land use. Science. 309: 570–574.

Forman RTT (2000) Estimate of the area affected ecologically by the road system in the United States. Conservation Biology. 14: 31–35.

Forman RTT and Alexander LE (1998) Roads and their major ecological effects. Annual Review of Ecology, Evolution, and Systematics. 29: 207-231.

Forman RTT and Deblinger DR (2000) The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. Conservation Biology. 14: 36-46.

Forman RTT, Reineking B and Hersperger AM (2002) Road traffic and nearby grassland bird patterns in a suburbanizing landscape. Environmental Management. 29: 782-800.

Foster P (2001) The potential negative impacts of global climate change on tropical montane cloud forests. Earth-Science Reviews. 55: 73–106.

9 – References

Fraterrigo MJ and Wiens JA (2005) Bird communities of Colorado Rocky Mountains along a gradient of exurban development. Landscape and Urban Planning. 71: 263-275.

Gardner TA, Barlow J, Chazdon R, Ewers RM, Harvey CA, Peres CA and Sodhi NS (2009) Prospects for tropical forest biodiversity in a human-modified world. Ecology Letters. 12: 561–582.

Gareca EE, Hermy M, Fjeldsa J and Honnay O (2010) *Polylepis* woodland remnants as biodiversity islands in the Bolivian high Andes. Biodiversity and Conservation. 19: 3327–3346.

Girvan M and Newman MEJ (2002) Community structure in social and biological networks. Proceedings of the National Academy of Sciences of the United States of America. 99: 7821–7826.

Gómez JM, Nunn CL and Verdú M (2013) Centrality in primate-parasite networks reveals the potential for the transmission of emerging infectious diseases to humans. Proceedings of the National Academy of Sciences of the United States of America. 110: 7738–41.

Granizo T, Pacheco C, Ribadeneira MB, Guerrero M and Suárez L (eds.) (2002) Libro rojo de las aves del Ecuador, tomo 2. (Quito, Ecuador): SIMBIOE, Conservación Internacional, Eco-Ciencia, Ministerio del Ambiente, UICN Serie Libros Rojos del Ecuador.

Grass I, Berens DG and Farwig N (2014) Guild-specific shifts in visitation rates of frugivores with habitat loss and plant invasion. Oikos. 123: 575–582.

9 – References

Hannah L, Midgley G, Andelman S, Araújo M, Hughes G, Martinez-Meyer E, Pearson R and Williams P (2007) Protected area needs in a changing climate. Frontiers in Ecology and the Environment 5:131–138.

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A and Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. Science (New York, N.Y.). 342: 850–3.

Harden C and Borrero AL (2005) Report on the Geomorphology of Parque Nacional Cajas. Unpublished report. (Cuenca, Ecuador): Parque Nacional Cajas.

Herzog SK, Martínez R, Jørgensen PM and Tiessen H (2012) Cambio Climático y Biodiversidad en los Andes Tropicales. (Paris): Inter-American Institute for Global Research and Scientific Committee on Problems of the Environment.

Hofstede R, Coppus RP, Mena-Vásconez P, Segarra P, Wolf J and Sevink J (2002) El estado de conservación de los páramos de pajonal en el Ecuador. Ecotropicos. 15: 3-18.

Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate B a, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L and O'Connor MI (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature. 486:105–8.

IERSE (2004) Estaciones meteorológicas de la cuenca del río Paute. (Cuenca, Ecuador): Unpublished report. Universidad. del Azuay.

Jackson D (1993) Stopping Rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology. 74: 2204–2214.

9 – References

Johnson AR, Wiens JA, Milne BT and Crist TO (1992) Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology. 7: 63–75.

Jordán F, Benedek Z and Podani J (2007) Quantifying positional importance in food webs: a comparison of centrality indices. Ecological Modelling. 205: 270–275.

Jørgensen PM and S León-Yánez (eds.) (1999) Catalogue of the vascular plants of Ecuador. Monogr. Syst. Bot. Missouri Bot. Gard. 75: i–viii, 1–1182.

Kattan GH, Franco P, Saavedra-Rodríguez CA, Valderrama C, Rojas V, Osorio D and Martínez J (2006) Spatial components of bird diversity in the Andes of Colombia: implications for designing a regional reserve system. Conservation Biology. 20: 1203–11.

Kociolek VA and Clevenger PA (2011) Effects of paved roads on birds: a literature review and recommendations for the Yellowstone to Yukon ecoregion. (Alberta, Canada): Yellowstone to Yukon Conservation Initiative, Canmore.

Koh LP and Ghazoul J (2010) A matrix-calibrated species-area model for predicting biodiversity losses due to land-use change. Conservation Biology 24:994–1001.

Krabbe N, Skov F, Fjeldså J and Petersen IK (1998) Avian diversity in the Ecuadorian Andes. An atlas of distribution of Andean forest birds and conservation priorities. DIVA Technical report. 4.(Rønde): Centre for Research on Cultural and Biological Diversity of Andean Rainforests.

Latta SC, Tinoco BA, Astudillo PX and Graham CH (2011) Patterns and magnitude of temporal change in avian communities in the Ecuadorian Andes. Condor. 113: 24–40.

9 – References

Laurance SGW (2004) Response of understory rain forest birds to road edges in central Amazonia. Ecological Applications. 14: 1344-1357.

Laurance WF, Sayer J and Cassman KG (2013) Agricultural expansion and its impacts on tropical nature. Trends in Ecology & Evolution. 1–10.

Leck CF (1979) Avian extinctions in an isolated tropical wet-forest preserve, Ecuador. Auk. 96: 343–352.

Lichstein J, Simons T, Shriner S and Franzreb K (2002) Spatial autocorrelation and autoregressive models in ecology. Ecological Monographs. 72: 445–463.

Lloyd H (2008a) Abundance and patterns of rarity of *Polylepis* birds in the Cordillera Vilcanota, southern Perú: implications for habitat management strategies. Bird Conservation International. 18: 164–180.

Lloyd H (2008b) Influence of within-patch habitat quality on high-Andean *Polylepis* bird abundance. Ibis. 150: 735–745.

Lloyd H and Marsden SJ (2008) Bird community variation across *Polylepis* woodland fragments and matrix habitats: implications for biodiversity conservation within a high Andean landscape. Biodiversity and Conservation. 17: 2645-2660.

Lloyd H and Marsden SJ (2011) Between-Patch Bird Movements within a High-Andean *Polylepis* Woodland/Matrix Landscape: Implications for Habitat Restoration Ecology. 19: 74–82.

MAE (2011) Subsistema Patrimonio de Áreas Naturales del Estado (PANE) de Ecuador. (Quito, Ecuador): Ministerio del Ambiente del Ecuador <http://www.ambiente.gob.ec/ ?q=node/59> (accessed 8 October 2014)>.

9 – References

MAE (2012) Línea base de deforestación del Ecuador continental. (Quito, Ecuador): Ministerio del Ambiente del Ecuador <http://sociobosque.ambiente.gob.ec/files/Folleto%20mapa-parte1.pdf> (accessed 8 October 2014).

Mateo RG, de la Estrella M, Felicísimo ÁM, Muñoz J and Guisan A (2013) A new spin on a compositionalist predictive modelling framework for conservation planning: A tropical case study in Ecuador. Biology Conservation. 160: 150–161.

Matson E and Bart D (2013) Interactions among fire legacies, grazing and topography predict shrub encroachment in post-agricultural páramo. Landscape Ecology. 29: 1829-1840.

Matson E and Bart D (2014) Plant-community responses to shrub cover in a páramo grassland released from grazing and burning. Austral Ecology. in press. DOI:10.1111/aec.12157

Mckinney ML and Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. TREE. 14: 450–453.

Mena-Vásconez P and Ortiz D (2004) Páramo. (Quito, Ecuador): Grupo de Trabajo en los Páramos del Ecuador.

Mena-Vásconez P and Hofstede R (2006) Los páramos ecuatorianos. In Botánica Económica de los Andes: 91-109. Morales M, Øllgaard B, Vist LP, Borchsenius F and Balslev H. (eds.). (La Paz, Bolivia): Universidad Mayor de San Andrés

Minga D and Verdugo A (2007). Riqueza florística y endemismo del Parque Nacional Cajas. Unpublished report. (Cuenca, Ecuador): Herbario Azuay, Universidad del Azuay.

9 – References

Minga D, Verdugo A, Ansaloni R and Izco J (2013) Diversidad fitocenótica en el Parque Nacional Cajas, Azuay, Ecuador. Unpublished report. (Cuenca, Ecuador): Herbario Azuay, Universidad del Azuay.

Moonen A-C and Bàrberi P (2008) Functional biodiversity: an agroecosystem approach. Agriculture, Ecosystems & Environment. 127: 7–21.

Mulwa RK, Böhning-Gaese K and Schleuning M (2012) High Bird Species Diversity in Structurally Heterogeneous Farmland in Western Kenya. Biotropica. 44: 801–809.

Myers N, Mittermeir RA, Mittermeir CG, da Fonseca GAB and Kent J (2000) Biodiversity hotspots for conservation priorities. Nature. 403: 853-858.

Nagendra H, Munroe DK and Southworth J (2004) From pattern to process: landscape fragmentation and the analysis of land use/land cover change. Agriculture, Ecosystems and Environment.101:111–115.

Neill DA. (1999) Vegetación. Pp. 13-25 In: Jørgensen PM and León-Yánez S (eds.) Catalogue of the vascular plants of Ecuador. Monogr. Syst. Bot. Missouri. Bot. Gard. 75.

Neuschulz E, Botzat A and Farwig N (2011) Effects of forest modification on bird community composition and seed removal in a heterogeneous landscape in South Africa. Oikos. 120: 1371–1379.

Neuschulz E, Brown M and Farwig N. (2013) Frequent bird movements across a highly fragmented landscape: the role of species traits and forest matrix. Animal Conservation. 16: 170–179.

9 – References

Nur N, Jones SL and Geupel GR (1999) A statistical guide to data analysis of avian monitoring programs. (Washington, D.C): U.S. Department of the Interior, Fish and Wildlife Service.

Oksanen J (2011) Multivariate analysis of ecological communities in R: vegan tutorial. <cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf>. (accessed 15 September 2014).

Oksanen J, Blanchet FG, Kindt R, Legendre R, Michin PR, O´hara RBG Simpson L, Solymos P, Stevens MHH and Wagner H (2011) Vegan: community ecology package. <www.CRAN.R-project.org/package=vegan>. (accessed 15 September 2014).

Ortega KY and Capen DE (1999) Effects of forest roads on habitat quality for ovenbirds in a forested landscape. Auk. 116: 937-946.

Palomino D and Carrascal LM (2007) Threshold distances to nearby cities and roads influence the bird community of a mosaic landscape. Biological Conservation. 40: 100-109.

Pardini R, Bueno ADA, Gardner T a, Prado PI, Metzger JP (2010) Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS One 5: 1-10.

Poulsen BO, Krabbe N (1998) Avifaunal diversity of five high-altitude cloud forests on the Andean western slope of Ecuador: testing a rapid assessment method. Journal of Biogeography. 25:83–93.

Purcell J and Brelsford A (2004) Reassessing the causes of decline of *Polylepis*, a tropical subalpine forest. Ecotropica. 10: 155–158.

9 – References

R Development Core Team. (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <www.R-project.org>. (accessed 15 September 2014).

Ralph CJ, Geupel R, Pyle P, Martin TE and DeSante DF (1993) Handbook of field methods for monitoring landbirds. (Bolinas, CA): Pacific Southwest Research Station, Forest Service, Department of Agriculture.

Ramsar Convention (2013) The Annotated Ramsar List: Ecuador. www.ramsar.org (accessed 23 June 2013).

Reijnen R and Foppen R (1994) The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for Willow Warblers (*Phylloscopus trochilus*) breeding close to a highway. Journal of Applied Ecology. 31: 85-94.

Reijnen RR, Foppen R and Veenbaas G (1997) Disturbance by traffic of breeding birds: evaluation of the effect and considerations in planning and managing road corridors. Biodiversity and Conservation. 6: 567-581.

Remsen Jr JV, Cadena CD, Jaramillo A, Nores M, Pacheco JF, Pérez-Emán Robbins MB, Stiles FG, Stotz DF and Zimmer KJ Version 31 October (2013) A classification of the bird species of South America. American Ornithologists' Union <www.museum.lsu.edu/~Remsen/SACCBaseline.html> (accessed 25 November 2013).

Renison D, Cingolani AM, Suarez R, Menoyo E, Coutsiers C, Sobral A and Hensen I (2005) The Restoration of Degraded Mountain Woodlands: Effects of Seed Provenance and Microsite Characteristics on Polylepis australis Seedling Survival and Growth in Central Argentina. Restoration Ecology. 13: 129–137.

9 – References

Ridgely R and Greenfield P (2001) The Birds of Ecuador: Field Guide. Ithaca (New York): Cornell University Press.

Robichaud I Villard M-A and Machtans CS (2002) Effects of forest regeneration on songbird movements in a managed forest landscape of Alberta . Landscape Ecology. 17: 247–262.

Robinson WD and Sherry TW (2012) Mechanisms of avian population decline and species loss in tropical forest fragments. Journal Ornithology. 153: 141–152.

Rodríguez S (2008) Plan de zonificación y manejo recreacional y turístico del Parque Nacional Cajas. (Cuenca, Ecuador): Empresa Municipal de Telecomunicaciones, Agua Potable, Alcantarillado y Saneamiento Ambiental de Cuenca.

Rodríguez-Pérez J, García D and Martínez D (2014). Spatial networks of fleshy-fruited trees drive the flow of avian seed dispersal through a landscape. Functional Ecology. 28: 990–998.

Sala OE, Chapin III FS, Armesto JJ, Berlow E, Bloomfield J, Rodolfo Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M and Wall DH (2000) Global Biodiversity Scenarios for the Year 2100. Science. 287: 1770–1774.

Samaniego GM, Nieto A, Astudillo PX, Graham CH, Latta SC and Tinoco BA (2013) Influencia de la ganadería en la comunidad de aves de páramo en el Parque Nacional Cajas. Universidad Verdad 60: 43-70.

Sarmiento FO (2000) Breaking Mountain Paradigms: Ecological Effects on Human Impacts in Man-aged Tropandean Landscapes. A Journal of the Human Environment. 29:423–431.

Sarmiento FO and Frolich LM (2002) Andean Cloud Forest Tree Lines. Mountain Research and Development. 22:278–287.

Sekercioglu C (2006) Increasing awareness of avian ecological function. Trends in Ecology and Evolution. 21: 464–471.

Sierra R (ed.) (1999) Propuesta preliminar de un sistema de clasificación de vegetación para el Ecuador continental. (Quito, Ecuador): Proyecto INEFAN/GEF-BIRF y EcoCiencia.

Sierra R, Campos F and Chamberlin J (1999) Áreas prioritarias para la conservación de la biodiversidad en el Ecuador Continental. (Quito, Ecuador): Ministerio del Ambiente, Proyecto INEFAN/ GEF- BIRF, EcoCiencia y Wildlife Conservation Society.

Sodhi, S. N., L. H. Liow FAB (2004) Avian extinctions from tropical and subtropical forest. Annual Review of Ecology, Evolution, and Systematics. 35: 323–345.

Stattersfield AJ, Crosby MJ, Long AJ and Wege DC (1998) Endemic bird areas of the world: priorities for biodiversity conservation. (Cambridge, UK): BirdLife Conservation Series No. 7, BirdLife International.

Stotz DF, Fitzpatrick W, Parker TA and Moskovits DK (1996) Neotropical birds: ecology and conservation. (Chicago, IL): University of Chicago Press.

Su JC, Debinski DM and Jakubauskas ME (2004) Beyond Species Richness: Community Similarity as a Measure of Cross-Taxon Congruence for Coarse-Filter Conservation. Conservation Biology. 18: 167–173

9 – References

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M and Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography. 31: 79–92.

Tinoco BA and Astudillo PX (2007) Guía de campo de las aves del Parque Nacional Cajas. (Cuenca, Ecuador): ETAPA.

Tinoco BA, Astudillo PX, Latta SC, Strubbe D and Graham CH (2013) Influence of patch factors and connectivity on the avifauna of fragmented *Polylepis* Forest in the Ecuadorian Andes. Biotropica. 45: 602–611.

Ulloa C, Álvarez S, Jørgensen PM and Minga D (2004) Guía de 100 plantas silvestres del páramo del Parque Nacional Cajas. (Cuenca, Ecuador): ETAPA.

Verboom J, Foppen R, Chardon P, Opdam P and Luttikhuizen P (2001) Introducing the key patch approach for habitat networks with persistent populations: an example for marshland birds. Biological Conservation. 100: 89–101.

Vergara PM, Pérez-Hernández CG, Hahn IJ and Jiménez JE (2013) Matrix composition and corridor function for austral thrushes in a fragmented temperate forest. Landscape Ecology. 28: 121–133.

Watson SJ, Watson DM, Lucky GW and Spooner PG (2014) Effects of landscape composition and connectivity on the distribution of an endangered parrot in agricultural landscapes. Landscape Ecology. 29: 1249–1259.

Wege CD and Long A (1995) Key areas for threatened birds in tropics. (Cambridge, UK): BirdLife International.

Zar J (1984) Biostatistical analysis, second edition. Prentice Hall. Englewood Cliffs (NJ).

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Curriculum Vitae

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